FOSSIL SUIDAE FROM KANAPOI AND LOTHAGAM, NORTHWESTERN KENYA

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Abstract. During 1965–1968, expeditions from the Museum of Comparative Zoology, Harvard University, discovered and worked three deposits of fossiliferous sediments in the area southwest and west of Lake Rudolf, northwestern Kenya. One of these, Ekora, furnished relatively little material, but good assemblages came from Kanapoi and Lothagam. Fossil Suidae are fairly abundant and the material includes a number of excellent skulls and mandibles. Most of the suid specimens are assigned to the genus *Nyanzachoerus*, first recorded by L. S. B. Leakey in 1958 from Kanam, Kavirondo Gulf, Kenya. The most abundant Kanapoi suid is here named *Nyanzachoerus pattersoni*, differing from the type species *N. kanamensis* mainly in having stouter cheek teeth and a shorter diastema. A second Kanapoi species has much enlarged low-crowned third molars, with folded enamel, and it is named *N. plicatus*. The third new species, *N. tulotos*, is not present at Kanapoi but is distributed throughout the thick Lothagam-1 sequence. Its third molars are smaller than in the other species but the third and fourth premolars are larger; enlarged third and fourth premolars are one of the significant features of *Nyanzachoerus*. The upper canines have closed or nearly closed roots; the lower canines tend to be U-shaped towards the base. The skulls resemble *Hylochoerus* in general size and morphology but the braincase is more elevated. There is strong sexual dimorphism and the zygomatic arches are expanded, developing hollow bony protuberances or bosses in the male. A few fragments, which may be *N. pattersoni*, occur in Lothagam–1 and *N. plicatus* occurs in

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Lothagam–3. Only *N.* cf. *plicatus* occurs at Ekora, which is stratigraphically younger than Kanapoi. At Kanapoi there are scraps of a very large *Notochoerus*, possibly close to *N. capensis* Broom, and a smaller form resembling the Kaiso species *N. euilus* Hopwood; the latter also occurs in Lothagam–3 and is known to occur in the lower Omo beds (Shungura Formation). Both *N. pattersoni* and *N. plicatus* occur in the Mursi Formation ("Yellow Sands") in the Omo area, dated at 4.05 million years. The Lothagam beds are cut by a basalt dated at 3.71 million years, thus providing a minimum age for the entire sequence. The Ekora Beds are estimated to be a little younger than the Mursi Formation, which must be closely equivalent to the Kanapoi beds and Lothagam–3. The base of the Lothagam sequence is probably close to 5.5 million years. Correlations with other formations are suggested.

INTRODUCTION

Since the publication of Leakey's survey of the East African fossil Suidae (1958), a substantial amount of new material has been recovered from various deposits in this region, in many cases including more complete specimens that make it possible to modify or extend earlier work. In particular, a recently discovered deposit at Kanapoi, southwest of Lake Rudolf in northwestern Kenya, has yielded suid material that probably constitutes the finest collection yet found at any single fossil locality in Africa. There are a number of well-preserved skulls, some of them almost complete, and good lower dentitions also. Another new locality at Lothagam Hill, 40 miles north of Kanapoi, has furnished a single complete skull, a number of mandibles, and other remains. It would appear from a close study of the collections that most of the material from these two deposits must be assigned to the genus *Nyanzachoerus,* of which there are two very different new species at Kanapoi and a third new one at Lothagam. The specimens extend greatly our knowledge of this extinct genus. Other genera and species of Suidae are represented both at Kanapoi and at Lothagam, but the material is scanty and incomplete so that specific diagnosis is difficult. Although this account deals with all the suid remains from these sites, it is concerned mainly with *Nyanzachoerus.*

The Kanapoi locality (Fig. 1) was discovered in 1965 by an expedition from the Museum of Comparative Zoology, Harvard University, which had been working for several years in the Miocene beds of Turkana, northwestern Kenya. A short general account of the local geology and preliminary list of the fauna was published by the leader of the expedition, Professor Bryan Patterson (1966), and the age of the deposit was tentatively assessed as early Pleistocene (Villafranchian). The base of the sediments is not exposed, but the sequence consists of more than 200 feet of material ranging from clays to conglomerates. A lower division of clays, silts and some sandstones can be recognised, and appears to be essentially lacustrine in origin; nearly all the suid material came from these deposits. The upper division consists mainly of coarser clastic debris mixed with layers of finer sediments and it is probably fluviatile in origin. Capping the sediments is a basaltic lava, with reversed magnetic polarity. Samples from one spot have provided potassium-argon ages of 2.5 ± 0.2, 2.9 ± 0.3, and 2.71 ± 0.26 million years (Patterson, Behrensmeyer and Sill, 1970). The fossil material includes the distal end of a hominid humerus (Patterson and Howells, 1967), which is possibly *Australopithecus* (but not *Paranthropus*). As will be discussed later, the faunal evidence suggests an age for the sediments considerably greater than that given by the Kanapoi basalt, although there is no field evidence for any erosion interval below the lava, nor was evidence seen to suggest that it is intrusive. (See footnote on page 226.)

The Kanapoi sediments and the overlying basalt were traced northeastwards for about 15 miles to Ekora (Fig. 1). At this locality only the uppermost Kanapoi beds are exposed but the basalt is overlain by a group of silty to gritty sediments, the top of the sequence being concealed. Some

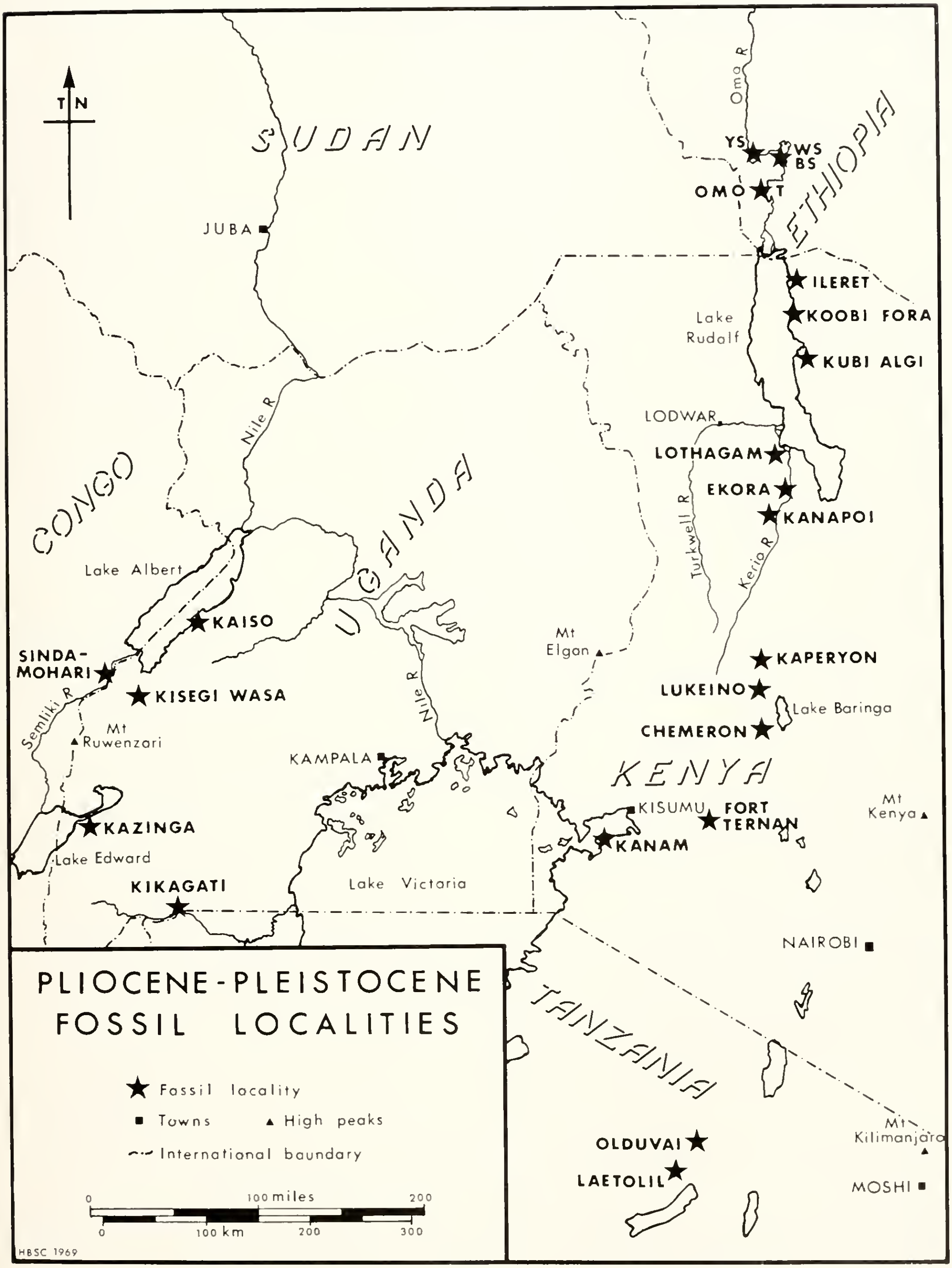

Figure 1. Map of part of East Africa to show the principal Pliocene-Pleistocene fossil localities. In the Omo area, north of Lake Rudolf, the abbreviations used are as follows: T—type area (Shungura Formation); WS—"White Sands" and BS—"Brown Sands" (Usno Formation); YS—"Yellow Sands" (Mursi Formation).

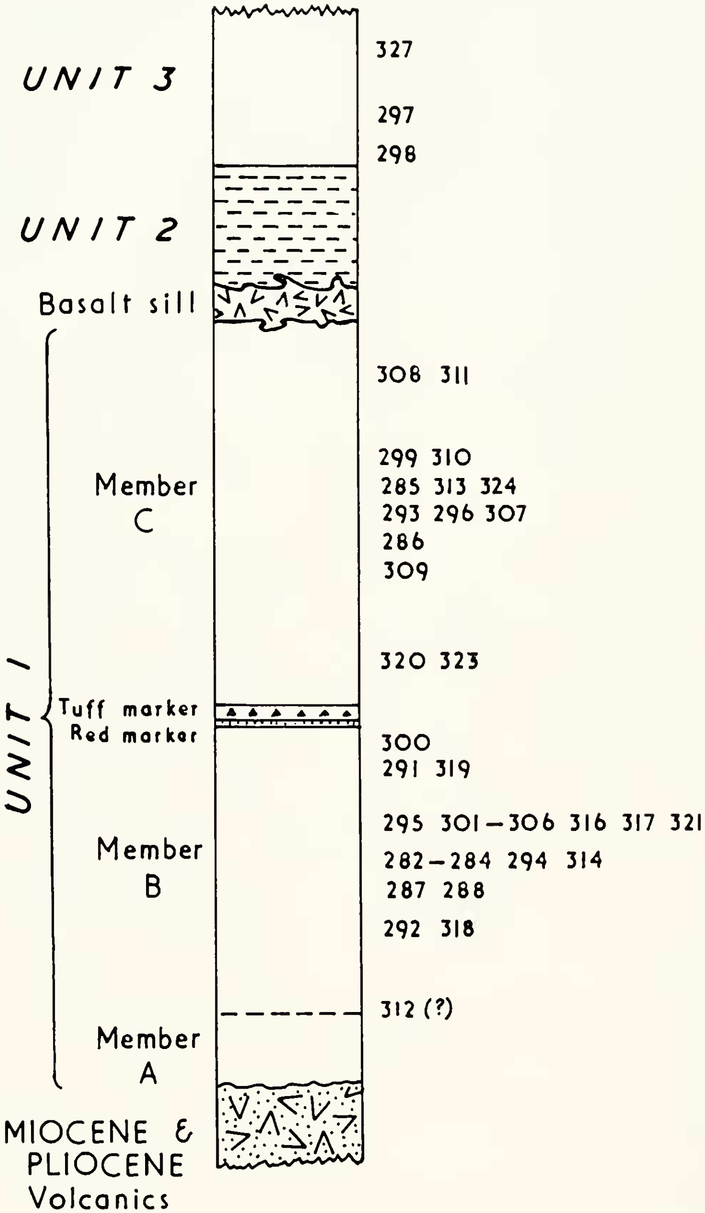

Figure 2. Composite columnar section of the Lothagam sequence, 2000 feet thick, showing the horizons from which the suid specimens were recovered. (*Stratigraphy after Miss A. K. Behrensmeyer.*)

excellent proboscidean remains were recovered from these Ekora beds, but only a few fragmentary suid specimens were found.

In 1967, the expedition continued its work in northwestern Kenya at another new locality at Lothagam Hill, some 40 miles north of Kanapoi on the west side of Lake Rudolf, not far from the deltas of the Kerio and Turkwell rivers (Fig. 1). The

TABLE 1. STRATIGRAPHIC DISTRIBUTION OF SUIDAE FROM LOTHAGAM, KANAPOI, AND EKORA

	LOTHAGAM				
	Unit 1 Memb. B	Unit 1 Memb. C	Unit 3	KANAPOI	EKORA
Nyanzachoerus pattersoni	cf.	cf.		x	
Nyanzachoerus plicatus		x	x	x	cf.
Nyanzachoerus tulotos	x	x			
Nyanzachoerus spp.	x	x		x	
Notochoerus cf. *capensis*				x	
Notochoerus cf. *euilus*			x	x	
Suidae indet.	x			x	

fossil material comes from several horizons within a thick sedimentary sequence that rests unconformably on Miocene/Pliocene lavas and associated boulder conglomerate. Hominid material was found but is undescribed (Patterson, personal communication). The area was mapped in 1967 by Dr. W. D. Sill and again, in more detail, in 1968 by Miss A. K. Behrensmeyer, who recognised three sedimentary units (Patterson et al., 1970). The lowest (Unit 1) is 800 to 1500 feet thick and consists of coarse conglomerate near the base (Member A), followed by irregular alternations of fine conglomerates, thinly bedded sandstones, silts, and occasional shales or tuffaceous shales. Near the middle of this sequence there is a conspicuous red silty band overlain by about 30 feet of tuff, which forms a useful "marker" horizon between the upper two members of the unit (see Fig. 2). The best suid material comes from Member B; the lower horizons of Member C furnished very little suid material, but these fossils were again moderately plentiful higher up. The beds of Unit 1 appear to represent fairly continuous and rapid deposition on an aggradational plain, probably a delta. Unit 2 comprises some 250 feet of lacustrine clays and silts, almost devoid of fossils; a fairly substantial time must have been involved in the deposition of this unit. Unit 3 comprises more than 300 feet of medium to coarse-grained clastic sediments, probably of fluviatile origin; the top of the sequence is concealed. Only a few fossils have come from these upper beds. The contact between the fluvio-deltaic deposits of Unit 1 and the lacustrine beds of Unit 2 is obscured by an intrusive basaltic sill, about 80 feet thick, so that their exact mutual relationship is uncertain. A potassium-argon age of 3.71 ± 0.23 million years has been obtained for this basalt, thus providing an upper limit for the age of the whole of the Lothagam succession (Patterson et al., 1970). Figure 2 gives a diagrammatic columnar section for the sequence and shows the horizons from which the principal fossil suid specimens were derived.

Table 1 lists the suids identified from Kanapoi, Lothagam, and Ekora. The whole assemblage suggests that the Kanapoi beds could not be older than the top of Unit 1 at Lothagam, but might be as young as the fluvial deposits of Unit 3. The Ekora beds are younger than the Kanapoi beds, but there is no reason to believe that a long gap intervenes. Even if the base of the Pleistocene extends back as far as 3.0 million years, the Ekora beds are probably Upper Pliocene. The Kanapoi beds must also be Upper Pliocene and Unit 1 at Lothagam Middle Pliocene.

THE GENUS *NYANZACHOERUS*

The type species of the genus, *Nyanzachoerus kanamensis*, was established by Leakey in 1958 and was based on three specimens from Kanam West, Kenya. The holotype is a left mandibular ramus having the canine and cheek teeth, but lacking incisors (British Museum Natural History [BMNH] no. M 15882). The first paratype is a fragment of a right mandibular ramus with RM_2 and RM_3 (Kenya National Museum, Nairobi [KNM]). The second paratype was an upper right third molar (BMNH M 16383) found 15 years later at the same site as the holotype and believed by Leakey possibly to belong to the same individual. However, the upper molar is well abraded, whereas the holotype M_3 is very little worn, so that this possibility can be excluded. Furthermore, the upper molar is rather short in relation to the lower third molars (42.5 mm as against 50.5 mm) and there is a good possibility that this tooth belongs to another species; it is, in fact, very close to the new Lothagam species, *N. tulotos,* in which the upper molars average 40.8 mm in length and the lowers 41.7 mm. Accordingly, the second paratype must be treated with caution and is here regarded as representing an undetermined suid, probably not *N. kanamensis.*

The genus was originally diagnosed by Leakey (1958) as follows:

> "A genus of Suidae with enlarged 3rd and 4th lower premolars resembling those of *Tetraconodon* Falc., but more laterally compressed. Upper and lower molars closer to those of *Sus* than of *Potamochoerus.* Lower canines of verrucose type."

The specific diagnosis for *N. kanamensis* was as follows:

> "A species of *Nyanzachoerus* of medium size and with the length of the dental series P_3 to M_3 greater than 150 mm. 2nd premolar much reduced, compared with the very large P_3 and P_4. The index $P_{3-4} \times 100/M_{1-3}$ above the range of *Sus* and *Potamochoerus.*"

The enlargement of the third and fourth premolars, which may be regarded as the essential basis for the establishment of the genus, is apparent in all the new material, both in the lower and in the upper dentitions. The second premolars are not correspondingly enlarged but retain about the size relationship to the molar teeth that is normal in *Sus* or *Potamochoerus;* they *appear* reduced because of the contrast in size to the adjoining third premolar. The enlargement of the premolars is not, in fact, very like that found in *Tetraconodon* (or in *Conohyus*), and there is no indication of any connection with the Indian forms. The degree of enlargement and the relative proportions of the teeth vary with the different species now recognized. A revised diagnosis for the genus and for the type species may now be given.

Class *MAMMALIA* Linnaeus 1758
Order **Artiodactyla** Owen 1848
Infraorder **Suina** Gray 1868
Family SUIDAE Gray 1821
Genus *Nyanzachoerus* Leakey 1958

Revised diagnosis. A genus of Suidae with cheek teeth similar to *Potamochoerus* in basic structure but tending to be more hypsodont and with main cusps of molars more distinctly columnar; third and fourth premolars relatively enlarged and more hypsodont than in *Potamochoerus.* Lower fourth premolar with three roots. Incisors similar to those of *Potamochoerus.* Upper canines oval to flattened oval in cross section, bearing little or no enamel, and with closed or nearly closed roots. Lower canines U-shaped or heart-shaped in cross section near the base, becoming more verrucose or triangular towards the tip; thin, weakly grooved enamel on two lateral faces; roots partially closed or open. Strong sexual dimorphism exhibited in size of canines and massiveness of skull; hollow bony protuberances or bosses on zygomatic arches present in male, weak or absent in female. Corpus of mandible heavy and contrasting markedly with unusually thin bone forming the angle.

Type species: *Nyanzachoerus kanamensis* Leakey 1958.

Nyanzachoerus kanamensis Leakey

Nyanzachoerus kanamensis Leakey, 1958: 4, pl. 1.

Revised diagnosis. A species of *Nyanzachoerus* somewhat larger than the extant *Hylochoerus.* Lower third molar with three pairs of lateral pillars and small to moderate posterior pillar on the talonid; length about two and one-fourth times breadth. Molars brachyodont, less columnar in structure, and relatively narrower than in *N. pattersoni.* Premolar series (P_2–P_4) about 60 per cent of the length of the molar series; P_3 more than half the length of M_3 and narrow, with length/breadth ratio about 1.9; P_4 shorter and wider than P_3, with length/breadth ratio about 1.3. Diastema from canine to P_2 substantially longer than length of premolar series P_2–P_4. P_1 apparently absent. Upper dentition not certainly known.

Holotype. BMNH M 15882: left mandibular ramus with canine and cheek teeth, but lacking incisors.

Paratype. KNM-KW: fragment of right mandibular ramus with RM_2 and RM_3.

Locality. Kanam West, Kavirondo Gulf, Kenya.

Horizon. Probably Plio-Pleistocene or Upper Pliocene.

Remarks. There is a considerable resemblance between the lower dentitions of *N. kanamensis* and the new Kanapoi species *N. pattersoni.* In the latter, however, P_3 is shorter and wider, having a length/breadth index of about 1.3 (instead of 1.9), and P_4 is slightly longer, but stouter, than the corresponding tooth in *N. kanamensis.* M_1 and M_2 have about the same width in the two species, but these two molars are longer in *N. kanamensis* than in *N. pattersoni.* In keeping with the relatively narrower and more elongate cheek teeth in *N. kanamensis,* the mandible is also more elongate and the diastema between P_2 and the back of the alveolus of the lower canine is much longer than in *N. pattersoni* (67.5 mm compared with 48–50 mm).

TWO NEW NYANZACHOERUS SPECIES FROM KANAPOI

Nyanzachoerus pattersoni sp. nov.*

Text-figures 3–6; Plates 1–9

Diagnosis. A species of *Nyanzachoerus* somewhat larger than the extant *Hylochoerus.* First premolars vestigial or absent. P^4 considerably narrower than M^3. Upper third molar with two pairs of lateral pillars and talon, length about 1.6 times breadth; brachyodont, maximum height of unworn third molar approximately 70 per cent maximum breadth. Lower third molar with three pairs of lateral pillars and stout posterior pillar, length about twice breadth. P_3 and P_4 robust, with length/breadth ratios of about 1.3 and 1.1 respectively. P_4 about two-fifths as long as M_3. Diastema from lower canine to P_2 substantially shorter than length of the premolar series P_2–P_4. Upper and lower premolar series (P2–P4) 60–70 per cent of the length of the molar series. In the male, maxillary flanges present round the bases of the canines but not particularly strongly developed; opposite the flanges there are slight thickenings at the level of the nasopremaxillary suture. Zygomatic protuberances extremely large in the male; towards the back they are deep dorsoventrally, appearing pear-shaped when viewed from the side, with lower margin not horizontal but curving downwards to approximately the level of the palatal plane. Female without maxillary flanges and with reduced zygomatic protuberances.

Holotype. KNM–KP 239: almost complete skull and associated mandible of adult female, together with the atlas and a damaged thoracic vertebra.

Paratype. KNM–KP 264: damaged skull and associated incomplete mandible of old male.

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* *N. pattersoni* has been referred to in several preliminary faunal lists as *Nyanzachoerus* species "A."

Locality. Kanapoi, northwestern Kenya.

Horizon. Kanapoi sediments; probably Upper Pliocene.

REFERRED SPECIMENS

Cranial (in approximate order of dental age). KNM–KP 222: fragment of right maxilla with Rdm^4 and part of RM^1. KP 244: almost complete skull of immature (subadult) individual with M^3 in alveolus; back of occiput missing. KP227: part of skull of immature (subadult) individual with M^3 in alveolus; cranium and snout missing. KP223: incomplete skull of young adult; occiput and snout missing. KP201: part of right maxilla of young adult with cheek teeth preserved. KP231: incomplete snout and partial palate of old female, lacking teeth except part of RM^3 and base of left canine.

Mandibular (in approximate order of dental age). KNM–KP 221: parts of left and right mandibular rami with milk teeth and RM_1. KP 266: part of left mandibular ramus with canine, milk teeth, RM_1 and RM_2. KP 213: part of left mandibular ramus of subadult with LP_3–M_2 and LM_3 partly erupted. KP 255: part of left mandibular ramus of young adult with LP_4–M_2. KP 256: part of right mandibular ramus of young adult with RP_4–M_3. KP 263: part of left and right mandibular rami of adult with LP_3–M_3 and roots of RP_2–M_3. KP 240: parts of left and right mandibular rami of adult with LM_2–M_3, RM_3 and roots of anterior cheek teeth. KP 258: part of left mandibular ramus of adult with LM_3 and roots of LP_4–M_2; fragment of right mandibular ramus without teeth. KP 219: damaged mandible of old individual; incisors and canines broken or missing. KP 259: part of left mandibular ramus of an old individual with LM_2 reduced to dentine and LM_3 almost patternless.

Cheek teeth. A number of isolated and fragmentary teeth are referred to this species; of these measurements only on the following are included in the tables: KNM–KP 205 (RM_1 and LM^2); KP 220 (RM_2); KP 228 (RM_1); KP 260 (RM_2).

Postcranial. KNM–KP 215: left tibia, some bones of the left pes and right manus, associated with tooth fragments and a right lower canine. KP 243: right tibia and right third metatarsal.

DESCRIPTION

The Holotype Skull and Mandible

The holotype skull (KNM–KP 239) is unusually well preserved, the only major damage being the loss of the nasals and the roof of the skull. The occipital crests are missing and the left zygomatic arch is incomplete. The tip of the premaxilla on the left side is lost, but two of the three incisors are present on the right side, as well as the socket for the third incisor. Both canines are preserved and the cheek teeth on both sides are intact (Pl. 1). Associated with the skull, and fitting to it, is a well-preserved mandible, with a few of the cheek teeth intact and others damaged (Pls. 2, 5).

The skull is about the same size as that of *Hylochoerus* and closely resembles the latter in general architecture. The zygoma, however, is more inflated, like that of *Phacochoerus* and the snout is rather more like that of *Sus* or *Potamochoerus.* The vertex length is estimated to have been approximately 480 mm and the zygomatic breadth was about 270 mm compared with 430 and 250 mm respectively in *Hylochoerus.* The vertical height of the crest of the occiput above the palatal plane was approximately 15–20 mm more than in the forest hog, but this is about in proportion to the rest of the skull. The muzzle is rather narrower, the width across the maxillae between the front edges of the infraorbital foramina being only about 50 mm compared with 70 mm in *Hylochoerus.* In the forest hog this foramen lies directly above the boundary between M^1 and M^2; in the fossil it is directly above the back half of P^3. As in *Phacochoerus,* the back-

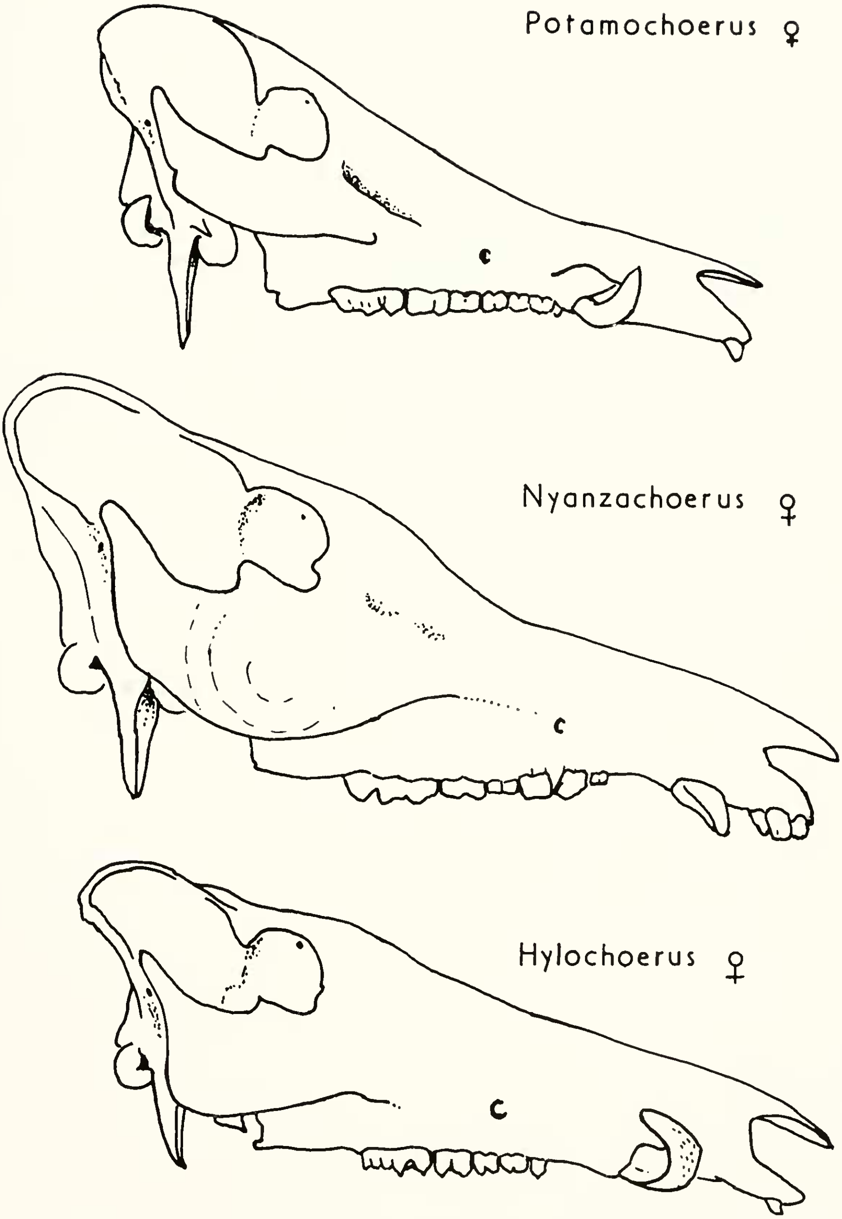

Figure 3. Reconstruction of the skull of the holotype (female) of *Nyanzachoerus pattersoni* (centre) compared with *Potamochoerus* (above) and *Hylochoerus* (below). The specimens are aligned on the front of the orbit and have the occlusal plane horizontal. × ¼.

ward flare of the maxillary portion of the zygomatic arch commences a good deal further forward than in *Hylochoerus*. The difference in contour will be seen in the comparative drawings in Figure 3. The effect is to make the braincase appear relatively longer and the snout shorter than in *Hylochoerus*. The "droop" of the snout below the plane of the cheek teeth is slightly exaggerated by fracturing, but was rather more pronounced than in *Hylochoerus* and less extreme than in *Phacochoerus*.

The back of the occiput, as far as it is preserved, is like that of *Potamochoerus* or *Phacochoerus* and there is no sign of the median vertical ridge that occurs in the forest hog. Although the occipital crests are lost and the upper part of the skull is damaged, it is clear that the crests were not quite as wide as in *Hylochoerus*. It is also clear that the contour of the frontoparietal region was flat or slightly depressed although not to the extent seen in *Hylochoerus* (described by Ewer [1958] as having "a highly characteristic collapsed appearance, like a badly baked cake"). The top of the braincase is higher and the slope of the frontoparietal region is a little steeper in the fossil than in the forest hog. The occipital condyles and glenoid cavity are relatively higher above the occlusal plane, although this is not nearly as exaggerated as in *Phacochoerus*. The glenoid itself is moderately wide from front to back, as in *Hylochoerus*, and is quite unlike the narrow transversely elongated bar found in *Phacochoerus*.

In correlation with the more elevated glenoid, the zygomatic portion of the squamosal slopes up more steeply from the jugal than in *Hylochoerus;* the external ear openings are considerably higher and the ascending ramus of the lower jaw must also have been higher in the fossil.

In *Hylochoerus*, both the jugal and the squamosal underlying the zygomatic wart are thickened to form a protuberance that breaks the smooth contour of the zygoma. As already noted, this thickening is exaggerated in the fossil, forming a distinct and rather knoblike dilation. Despite the fact that the inner surface of the zygoma is slightly hollowed out beneath it, the bone in the centre of the protuberance reaches a thickness of 32 mm; the jugal is also vertically much deeper than in *Hylochoerus*, the lower border of the expanded portion drooping considerably. Behind the rounded posterior margin of the 'knob,' however, the posterior part of the zygoma is extremely slender, as in *Potamochoerus*. As will be seen in the account of the paratype (Pls. 2 and 3), this zygomatic knob is excessively exaggerated in what is believed to be the male of the same species, the holotype being regarded as a female.

From the palatal aspect, the general resemblances to *Hylochoerus* are again apparent, in part because of the similar basic outline of the zygomatic arches. There are, however, a number of differences. The greater vertical distance between the palatal plane and the glenoids and occipital condyles has already been mentioned. The paramastoid processes would therefore be expected to be longer than in *Hylochoerus;* although the tips have been broken off, the robust basal portions suggest that this was indeed the case. The auditory bullae are slender and subtriangular in cross section and are much less inflated than those of *Hylochoerus*. The posterior ends of the palatines are damaged, but the parts that remain do not suggest any major difference from *Hylochoerus*. The palatine notch, however, is much narrower; in fact no wider than in *Potamochoerus*.

The general shape of the palate in the holotype is somewhat intermediate between that of *Hylochoerus* and *Potamochoerus*, largely because the fossil lacks the expanded bony buttresses that contain the roots of the canine teeth in the forest hog. However, the shape of the anterior part of the palate and premaxilla is like that of *Hylochoerus* in being expanded between the canines and in tapering both behind and in front of them, rather than being parallel-sided as in *Potamochoerus*. (In the larger male, as will be seen later, the palate is much more hylochoerine.)

The upper dentition is virtually complete. In life all three incisors were present, although the third incisor is missing from the holotype and is represented only by the root cavity, filled with matrix. The first and second incisors are both large teeth, almost equal in size; the alveolus of I^3 shows that this tooth also was large. The I^1 is well worn, but the shape of the dentine area suggests that its morphology was much the same as that of the less worn I^2. The latter tooth shows a structure comprising a broad anterior cone and a narrower posterior cone; on the posterointernal flank of the hinder cone are two small tubercles or conelets. In front of the foremost of these conelets, and thus lying on the lingual surface of the crown between the main cones, is a small fovea enclosed by a thin lingual ridge, almost like a weak cingulum. Comparison with the living African forms is not meaningful as the incisors in all three forms are specialized in one way or another; other comparisons are difficult to make as these teeth are seldom found in fossils. The structure of the incisors is very similar to that shown in the second premolar.

The upper canines are small, being comparable in size, position, and angle of emergence, with the corresponding teeth in *Potamochoerus*. As in the latter, there is an anterior wear facet that is practically at right angles to the axis of the skull. The bases of the canines were surrounded by thin extensions of the maxillary bone, but there is no indication of the vertical "wings" exhibited by *Potamochoerus*. Morphologically the canine is unlike that of *Potamochoerus, Sus,* or *Hylochoerus*. In cross section it is oval, slightly pointed anteriorly and flattened posteriorly, as well as slightly flattened dorsally and ventrally (see Fig. 5). This is similar to the shape found in the tips of very young canines of *Phacochoerus*. There is a thin coating of enamel, apparently confined to the tips of the teeth, and this is smooth except for weak longitudinal ridges or striations. The small size of the tusks, despite the fact that they belong to an adult animal, suggests that the canines have closed roots, or roots that are nearly closed. There is a strong morphological resemblance to the canines of "*Promesochoerus mukiri*" and "*Ectopotamochoerus dubius*" (Leakey, 1965), although there is no other close resemblance to those species.

There is a short diastema between the back of the canines and the front of the small second premolar. In the centre of this gap, on the left side, there is what might possibly be the mark of a root for a very small P^1, but it is not at all certain that this tooth was ever present; there is no corresponding mark on the other side. Relative to the molars, the third and fourth premolars are extremely large, as compared with those of *Sus* or *Potamochoerus*. The first molar is worn down to dentine, with only traces of enamel. The second molar is well worn, and the third molar is in moderate wear with the hindmost large cusp of the talon in early wear. The dentition thus represents a young adult, presumed to be female. The details of the cheek teeth will be included in the systematic account of the dentition.

The mandible, which fits the skull, lacks the left mandibular ramus behind the third molar and also the upper part of the ascending ramus on the right side. In size and general morphology, it is very similar to the jaw of *Hylochoerus*, being fairly thick in the corpus to a point anterior to the level of the back of the symphysis. However, the canines are relatively smaller than in *Hylochoerus* and, consequently, the symphysial region is not so broad and flat and is therefore somewhat like *Potamochoerus* in this respect. The arch of the incisors is intermediate between the condition in the two living forms.

All six incisors are present, and they correspond in size relationships and general morphology to those of *Potamochoerus*. As in the bushpig, there is a ridge along the posterior (upper) face of the enamel in each incisor, although in the fossil the ridge is more marked than in the bushpig, so that this aspect of the tooth is broadly triangular in section. The demarcation between the base of the enamel and the roots is more clearly marked than in *Potamochoerus*. The tips of the four central incisors are worn in a straight line at the front of the jaw, but the tips of the third incisors extend only to a position about half way along the body of the second incisor, as in *Potamochoerus*, and their tips are only slightly worn.

The lower canines are of the verrucose type and resemble those of *Hylochoerus* in being slightly convex on both lingual and buccal faces, lacking any indication of the broad concavity or groove typically present on the buccal face in *Potamochoerus*. The tooth is more compressed laterally than in *Potamochoerus* or *Hylochoerus* and the lingual face is only slightly longer than the buccal one. There is no enamel on the posterior face, even beyond the area of abrasion. The enamel is fairly thin and has the same texture as in *Potamochoerus*. The wear facet on the tip of the posterior face, matching that of the upper canines, is vertically oriented and at right angles to the long axis of the skull. It is virtually indistinguishable from the lower canine of "*Ectopotamochoerus dubius*" Leakey (1965).

Of the cheek teeth, the right third premolar, both second premolars and both third molars are preserved intact; the left third and fourth premolars are damaged posteriorly, and the left second molar is slightly damaged, but the remaining teeth are broken away. Details of the teeth are included in the systematic account of the dentition, given below. As the first molars are missing and the P_4 is damaged, the descriptions of these teeth are, of necessity, based on referred specimens.

The Atlas of the Holotype

Associated with the holotype skull were three vertebrae, a well-preserved atlas that fits the skull, a mid-thoracic vertebra, and an incomplete centrum. The thoracic vertebra is incomplete and in poor condition but corresponds reasonably closely with the seventh vertebra in *Hylochoerus*, both in size and general morphology.

Figure 4. Diagrammatic sagittal section of the roof of the neural canal in the atlas vertebrae of A, *Phacochoerus* and B, *Nyanzachoerus pattersoni*. The thick line shows the area of attachment of the rectus capitis dorsalis muscle. The arrow indicates the direction of the neural canal.

The atlas is very similar in size to that of *Hylochoerus* but is a little more massive in construction. The wings do not have the unusual, almost rectangular outline characteristic of *Phacochoerus* but are more rounded, as in *Potamochoerus* and *Hylochoerus*, the resemblance being closer to the latter. The fossil atlas is relatively deeper dorsoventrally than in any of the extant species, but this is due more to thickening of the bone and larger dorsal and ventral tuberosities than to enlargement of the neural canal or difference in shape of the articular facets. In none of the extant species is the ventral tubercle very large, whereas in the fossil there is a conspicuous downward conical bulge behind the rim of the anterior articular cavity, which tapers off towards the middle of the centrum. In the three extant species the atlas bears a roughened central area in the anterior region of the neural arch. This represents a somewhat tendinous attachment of the deepest fibres of the rectus capitis dorsalis muscle. In the warthog this roughened area is oriented almost at right angles to the line of the neural canal and to the plane of the wings of the atlas. The roof of the neural canal is therefore deeper at its anterior than at its posterior margin (Fig. 4a). In *Hylochoerus* there is considerable individual variation, but the roughened surface always slopes obliquely backwards so that it forms a more acute angle with the neural canal and the plane of the atlantal wings; its posterior margin forms a raised bump on the neural arch. The difference is presumably related to the carriage of the head, which is much more vertical in *Phacochoerus* than in *Hylochoerus*. In the fossil the condition is much as in *Hylochoerus*, with the facet sloping backwards so that its posterior margin lies midway between the anterior and posterior margins of the neural arch (Fig. 4b). Presumably this reflects the more or less normal carriage of the head in *Nyanzachoerus*.

The Paratype Skull and Mandible

The skull of the paratype (KNM–KP 264) is badly damaged at the back so that the entire basicranial region is lost. The frontal and orbital margins are damaged and the whole of the left zygomatic arch is missing. The right zygoma is fairly complete except in the temporal region. There is also an isolated fragment comprising a large part of the back of the parietal and occiput, with portions of the adjoining temporal areas. Unfortunately, it is incomplete and no direct contact with the skull remains. In the illustrations (Pls. 2 and 3) it has been placed in its approximate position. Also isolated is a fragment of the temporal around the external auditory meatus; it displays a long vertical process above the ear opening, even more developed than in *Hylochoerus*. The cheek teeth are partly preserved on both sides but are in very advanced wear and the anterior teeth are almost featureless; the premolars are broken off at the roots on the right side.

The skull is substantially longer than that of the holotype, with an estimated vertex length about 10 cm greater. The entire nasomaxillary region is very much wider than in the holotype and extremely like that of *Hylochoerus* in outline, but more massive. The basically *Hylochoerus*-like morphology is obscured by the fact that the jugal region is expanded into an enormous boss or protuberance so that the bizygomatic breadth is in the vicinity of 480 mm, i. e., 80 per cent of the vertex length, as compared with about 55 per cent in the holotype and in *Hylochoerus*. The animal's appearance in life must have been extraordinary. At first it was considered that this represented a species different from the holotype, but there are so many similarities in general morphology and in the dental characters that this consideration is most improbable. Accordingly, the specimen is now regarded as a large old male of the same species, and it is inferred that there was very strong sexual dimorphism. This point will be discussed in more detail later. Comparative measurements (including estimated measurements) on the two specimens are given in Table 2.

Although the supraorbital foramina lay in the missing portion of the braincase, the two grooves leading to them are present and these are flanked on the outer side by strong ridging as in *Hylochoerus*. However, in the forest hog the region between the grooves is raised and forms a rounded hump, which continues down the nasals; in the fossil, this area is flattened, as is also the nasal region generally. The flat nasal area meets the maxillae on either side at a fairly abrupt edge, like that in *Potamochoerus* (and in the holotype) so that the snout does not have the rounded contour seen in *Hylochoerus*. The bony flanges surrounding the upper tusks are very similar to those of *Hylochoerus*, as is also the shape of the premaxillary region. The zygomatic arch begins to flare out immediately behind the infraorbital foramen and the contours of the maxilla-lacrimal and maxilla-jugal regions correspond exactly to those in the holotype. As in the holotype, the anterior margin of the jugal protuberance slopes outwards and backwards to reach its maximal lateral extension at approximately the level of the orbit; from this point it turns in abruptly, so that the posterior margin is virtually at right angles to the skull and the protuberance does not extend back beyond the orbit. The ventral surface of the jugal is turned outwards, somewhat in the manner found in *Phaco-*

TABLE 2. MEASUREMENTS OF SKULLS OF *NYANZACHOERUS PATTERSONI* COMPARED WITH *HYLOCHOERUS MEINERTZHAGENI* AND *POTAMOCHOERUS PORCUS**

	Holotype KP 239 ♀	Paratype KP 264 ♂	Referred KP 231 ♀	*Hylochoerus* MA 1 H 1† ♂	*Potamochoerus* MA 1 Po 6† ♂
Vertex length	480 e	580 e		428	357
Basilar length	425	500 e		375	307
Bizygomatic breadth	c270	c480		246	171
Greatest breadth across nasals	53	71		56.5	60
Breadth of muzzle between infraorbital foramina	48	66	49	71	27
Parietal constriction		76		96	25.5
Palatal length	301	352		283	234
Palatine notch width	28.5	28.0	28	40.5	17.0
Breadth of palate					
— between $M^3 - M^3$	33	40	35	46	23.5
— between $P^2 - P^2$	52.5	73	59	59	38.5
Premaxilla breadth over $I^3 - I^3$	69	95		51.5	40.5
Diastema $I^3 - P^2$	72	101		119.5**	81.5
Diastema $C - P^2$	39.5	c35	c40	35.0	31.5
Length premolar series	51.9	68.0	c61.5	24.5	35.0***
Length molar series	95.2	99.1	c99.5	77.0	70.0
Length $P^2 - M^3$	147.0	161.6	c161.0	101.5	105.0***

* In this and all the subsequent tables, measurements are given in millimetres. The abbreviations "c" (for circa) is employed before a figure to indicate an approximate measurement; the abbreviation "e" is used after a figure to denote an estimated figure. A + sign following a figure indicates that the figure given is accurate but the original dimension was greater. "d" indicates tooth worn to dentine only.

** I^1 — P^2 *** omitting P^1

† Specimens in the osteology collection of the Kenya National Museum, selected as the best match for the relevant fossil material from the viewpoint of sex and dental age.

choerus, but its lower surface is damaged and details cannot be seen.

In the palate, in the region between the cheek teeth, there is very little difference from that of the holotype, and the palatine notch is of comparable size. However, anteriorly the palate widens to accommodate the enlarged canines and the premaxillae taper much more than in the holotype. Only the sockets of the six incisor teeth remain, and these are a little larger than in the holotype skull. The left canine is broken off in the plane of the palate but its outline is easily seen. The shape is oval with the ventral surface slightly flattened and the dorsal surface flattened and slightly grooved (Fig. 5). The elongation is anteroposterior as in the holotype skull. The long axis is thus oriented in the opposite direction to that in a *Hylochoerus* tusk and closely resembles the condition found in *Phacochoerus*, though not nearly as exaggerated. As far as can be determined, this portion of the canine at least is devoid of enamel. There is at the centre only a very small pulp cavity or root canal, and it is inferred that the roots are closed or nearly closed. Relative to the size of the skull, the canines are very modest in size and probably did not protrude more than 8–10 cm from the bony bosses. They emerged almost parallel to the palatal plane.

The cheek teeth are in a very advanced state of wear, all but the third molar being virtually patternless. The second premolar is a little larger than in the holotype. It is possible that P^1 was present on the left side in the middle of the diastema, as there is a scar in this position, but there is no similar indication on the right side. On the left side the crowns of the premolars are missing and only the roots remain. The third molars are in advanced wear. They are of approximately the same size as those of the holotype and have exactly the same cusp pattern, the only obvious difference being that the enamel is thicker.

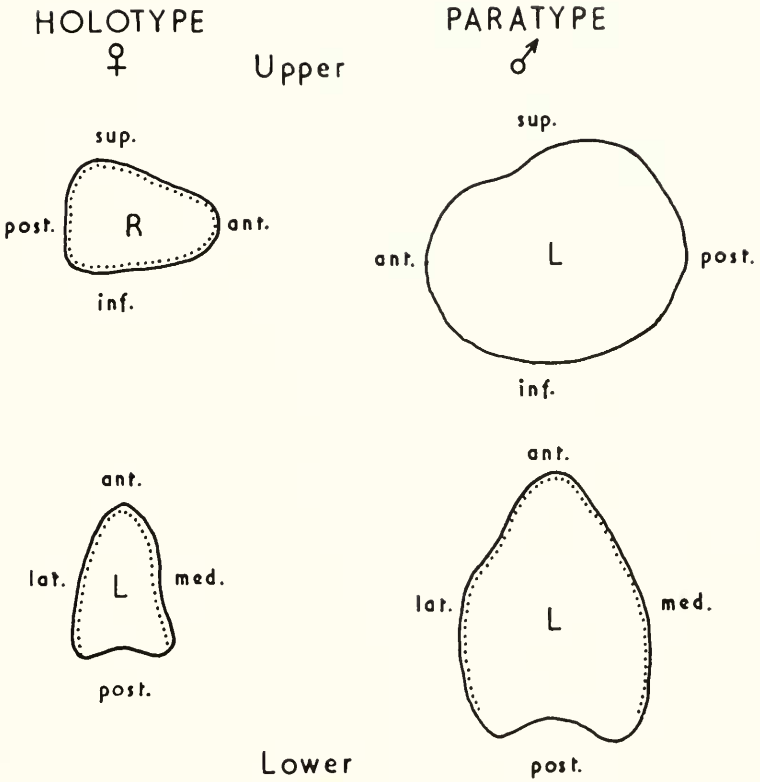

Figure 5. Sections through upper and lower canines of *Nyanzachoerus pattersoni*, near the border of the alveolus. The dotted line indicates the zone covered with enamel. Abbreviations: R—right; L—left; sup.—superior; inf.—inferior; ant.—anterior; post.—posterior; lat.—lateral; med.—median. All nat. size.

The isolated back portion of the cranium differs both from *Potamochoerus* and from *Hylochoerus*. The braincase between the temporal lines is flattened or smoothly concave, having neither the collapsed appearance of *Hylochoerus* nor the convexity of *Potamochoerus;* it is, indeed, a little like this region in *Phacochoerus*, suggesting that the orbits were slightly elevated, though not nearly as much as in the warthog. The skull clearly extended much further behind the orbits than it does in *Phacochoerus*. The back of the occiput is the same size as that of a large *Hylochoerus*, which means that, relative to the length of the skull, the occiput is somewhat narrower. The vertical median ridge, so conspicuous in *Hylochoerus*, is absent.

Associated directly with the skull, and undoubtedly belonging to the same individual, are the left and right mandibular rami. Both are broken off behind the third molars and through the canine alveoli; no part of the symphysis is preserved. The corpus is almost twice as thick as the mandible of the holotype and it is also considerably deeper. Of the cheek teeth, only the third molars remain intact, the anterior teeth being represented in the jaw only by roots; however, incomplete, well-worn second molars of both sides were found with this material and most probably belong to the same mandible. There are also three fragments of canines that do not quite join the pair in the jaw itself. The left canine is partly preserved within the jaw and it has a cross section of the verrucose type. The long axis is anteroposterior and the mesial (topographically dorsal) and lateral faces are almost equal in length. These faces are gently convex but are weakly grooved near the front so that there is a very slight anterior "keel." The posterior face has a broad groove, so that the cross section is almost heart-shaped (Fig. 5). The lateral faces are covered with thin enamel, which is very weakly striated; the posterior face has no enamel and the root, although open, is free of enamel.

Snout and Palate of Old Female

This partial skull (KP 231) was assembled from numerous fragments and represents the incomplete snout and palate of an old female. A fragment of third molar shows that the teeth were in an advanced stage of wear. The nasal area is broken at about the supraorbital foramina and the palate at the back of the palatine notch; the palate lacks the premaxillae and the front of the nasals. Unfortunately not possessing any actual contact, is an isolated fragment showing the back of the right orbit, the postorbital process and the parietal crest. This region is missing from the holotype but the fragment, which comes from a small-tusked and therefore presumably female skull, is virtually identical with the corresponding portion of the (assumed male) paratype. It is therefore of interest, as it lends further support to the identification of the holotype and paratype as the two sexes of a single species.

The right canine is missing but the left canine is broken off at about the margin of the alveolus. It is almost equidimensional, measuring 28.5 mm anteroposteriorly and 27.5 mm vertically. The upper surface is slightly flattened as also is the lingual surface. The pulp cavity, as in the paratype tusk, is extremely small, measuring only 10.5 × 6.7 mm on the broken surface. The bosses surrounding the canines are much less developed than in the old male skull but are decidedly larger than in the holotype. The breadth across the canines at their point of emergence from the alveolus is estimated to be about 125 or 130 mm as compared with 97 mm in the holotype and about 180–190 mm in the paratype.

The width across the muzzle at the infraorbital foramina is almost identical with that of the holotype (see Table 2), and the commencement of the outward flare of the zygomatic arch is also very similar to that of the holotype. In the holotype the nasal area is severely damaged by weathering and the form of the nasals cannot be determined. In this specimen, however, it can be seen that the nasals are flat but turn down rather sharply on either side to contact the premaxillae and maxillae below the level of the top of the snout. In transverse section, the shape of the snout would thus be a trapezoid with rounded corners. In this it differs from *Hylochoerus,* where the nasals turn down less sharply and form a continuous curve with the premaxillae and maxillae, so that the transverse section has the form of a simple arch, slightly flattened above.

Young Adult Skull

This specimen (KP 223) lacks the greater part of the braincase and occiput and also the palate and snout in front of the second premolars. The zygomatic arches are lost and the whole skull is crushed sideways and distorted. The third molars on both sides are preserved in an early stage of wear. In all the morphological features that can be studied, there is close agreement with those of the holotype. The frontoparietal area, which is badly damaged in the holotype, is partly preserved in this specimen, and the width across the parietals at the supraorbital processes is estimated to be 130–135 mm; the corresponding measurement for the holotype on a reconstruction is 130–140 mm. The parietal area is slightly concave between the supraorbital processes and the orbits are thus raised slightly above the mid-line of the frontoparietal area. This is very similar to the corresponding area in *Hylochoerus* but in the fossil the back part of the parietal rises instead of collapsing.

The Immature (Subadult) Skull

A well-preserved skull (KP 244) represents a subadult individual in which the second molars are in wear but the third molars are still unerupted. The fourth premolar is erupted to the level of the grinding surface and shows traces of wear, but the third premolars are incompletely erupted. There is no sign of a P^1. The right canine is broken off but the left is complete. It is newly erupted and the tip is bluntly rounded, without a wear facet. Even at this early stage, the tusk has a greater diameter than that of the holotype female, and there are already small bony bosses around the roots of the canines. There is a good possibility that this is the skull of a young male.

The rest of the skull agrees extremely well with the features shown in the holotype. The zygomatic arches are, unfortunately, missing on both sides. The roof of the skull is less damaged than in the other two specimens. The frontoparietal region is broad and flat. The area in front of the orbits continues the upward sloping plane of the snout but the area behind them is more nearly horizontally oriented. The contour of the skull therefore shows a slight angulation at the level of the orbits and does not run in an almost straight line from snout to occiput, as it does in *Potamochoerus*. The parietal constriction is much wider than in *Potamochoerus* of corresponding age, and the temporal line behind the orbits overhangs the braincase slightly. The upper margins of the orbits are broken, but they must have been level with the frontal surface or even have been very slightly elevated. The auditory bullae are somewhat peculiar, being slender, almost triangular in cross section and very pointed. The specimen is illustrated in Plate 10.

The lacrimal suture can be clearly seen, and the body of the lacrimal bone has the almost square shape found in *Potamochoerus* of similar age. The upper edge is prolonged into a fine tongue of bone running forward between the maxilla and the frontal, terminating just posterior to the nasal suture, very much as happens in *Phacochoerus*. The suture between the jugal and the maxilla slopes forwards and downwards from the anterior margin of the lacrimal as in *Phacochoerus*, whereas in both *Hylochoerus* and *Potamochoerus* the suture runs directly down in line with the front of the lacrimal. Thus, although the body of the lacrimal is short and *Potamochoerus*-like, the conformation of the sutures at the anterior end of the bone is phacochoeroid. This, presumably, is related to the inflation of the zygoma to form the large protuberance that has been described in the holo- and paratypes. Unfortunately the zygoma is not preserved and the juvenile condition of the zygomatic knob is therefore not shown. The anterior part of the jugal, forming the front of the arch is, however, preserved with little or no distortion on the right side of the skull. Both the jugal and the part of the maxilla anterior to it show the characteristic outward flare, and it is apparent that a zygomatic knob of some sort must have been present. We made a reconstruction of the zygoma on the assumption that the knob must end at the level of the back of the orbit, and refraining from making the knob itself any larger than is necessary in order to preserve a reasonably smooth contour on the outer surface. When this had been done, it was found that the knob, as restored, resembled very closely that of the holotype adult female. This is satisfactory, since it is to be expected that in a character showing strong sexual dimorphism an adult female should resemble a juvenile male. The restoration therefore lends support to the original opinion that the paratype and holotype represents the two sexes of a single species.

Mandible of an Old Individual

Specimen KP 219 is an almost complete mandible, presumed to belong to a male individual because of the relatively large sockets for the canines. The roots of four incisors are in position at the front of the symphysis, but the lateral area is broken away as far as the back of the canine sockets; the exact shape of the front of the mandible cannot be determined. The symphysis is long, being about the same length as the cheek teeth series. The lower border of the symphysis is in line with the middle of the fourth premolar. The symphysis is thus longer than in the holotype. The corpus of the mandible is very thick, although less massive than in the paratype (Pl. 4). The ascending ramus is broken off on the left side, and on the right the coronoid process and most of the condyles are missing; the angle, however, is preserved. In contrast to the heavy mandibular rami, the bone forming the angle is surprisingly thin. The lower border, although ridged internally—presumably in relation to the insertion of the internal pterygoid muscle—is not thickened along the outer margin. In this it resembles the mandible of *Potamochoerus* and differs from those of *Hylochoerus* and *Phacochoerus*.

All the cheek teeth are present. They are heavily worn but the characteristic enlargement of the premolars and typical pattern on the M_3 are clearly shown (Pl. 8). From the size and shape of the canine sockets, it is inferred that the canine was like that of the paratype, but a little smaller.

The Upper Dentition

The upper dentition is complete only in the holotype skull (KP 239). The cheek teeth are also intact in a fragment of skull that consists of the right maxilla from P^2 to M^3, together with the area above them up to the nasal suture line and the front of the jugal (KP 201). The cheek tooth series is also complete, but in very poor condition, on the right side of the palate of the paratype (KP 264). Partial series are present in two subadult skulls (KP 244, 227) and in the crushed skull of a young adult (KP 225). The overall measurements for the palate and dentition in the holotype and paratype have been given in Table 2. The range of variation in size, and average values for the upper cheek teeth are given in Table 3.

The cheek teeth are very similar to those of *Potamochoerus* in general structure but are slightly more hypsodont, and in the molars the main cusps are more distinctly columnar. The third and fourth premolars are decidedly more hypsodont in the fossil, as well as being relatively very much enlarged. In a subadult *Potamochoerus*, the height of P^4 is 91 per cent of the maximum breadth, compared with 114 per cent in the fossil; for M^2, the corresponding figures are 73 per cent in *Potamochoerus* and 87 per cent in the fossil. The third molar is slightly longer in proportion to its breadth than in the bushpig, but the lateral columns in the fossil are less massive, more conical, and better separated so that the crown does not have as compact an appearance. The talon is wider in the fossil. The enamel is actually only very slightly thicker than in *Potamochoerus* so that in proportion to the size of the crown it is relatively thinner, and the dentine areas in the enamel islands are therefore more conspicuous. Length/breadth ratios for a typical *Potamochoerus* are included in Table 3.

In the tooth measurements given in the tables that follow, "length" is the greatest length, measured on premolars across the cingulum just above the roots, on first and second molars on the occlusal surface, and on third molars from the front cingulum to the back of the talon; "breadth" is in

TABLE 3. AVERAGE DIMENSIONS OF UPPER CHEEK TEETH OF *NYANZACHOERUS PATTERSONI*

		Range	*N* *	*S.D.**	Mean	Typical *Potamochoerus*
P^2	length (L)	11.2 – 13.2	5	0.711	12.1	18.0
	breadth (B)	6.7 – 8.9	5	0.806	7.4	6.5
	L/B	1.48– 1.8			1.64	1.54
P^3	length	20.2 – 26.8	6	2.013	23.7	13.2
	breadth	18.5 – 20.8	6	1.126	19.8	10.5
	L/B	1.19– 1.30			1.22	1.26
P^4	length	18.0 – 20.3	7	0.950	19.1	13.0
	breadth	21.0 – 24.2	6	1.187	22.4	13.5
	L/B	0.80– 0.89			0.86	0.97
M^1	length	18.5 – 23.0	7	1.629	21.2	17.0
	breadth	17.3 – 20.1	5	0.958	18.8	16.5
	L/B	1.05– 1.19			1.13	1.03
M^2	length	26.3 – 32.0	9	2.006	28.7	22.0
	breadth	23.8 – 28.4	8	1.421	24.9	21.0
	L/B	1.12– 1.29			1.22	1.05
M^3	length	48.5 – 51.6	7	1.192	49.8	29.5
	breadth	28.8 – 32.4	6	1.231	31.2	20.5
	L/B	1.51– 1.73			1.60	1.44
$P^2 - P^4$		49.5 – 68.0	7	7.876	55.6	36.2
$M^1 - M^3$		96.0 –102.0	6	2.987	98.1	68.5
$P^2 - M^3$		146.1 –162.0	5	6.904	153.7	104.7
$\frac{P^2 - P^4}{M^1 - M^3}$		0.49– 0.71	5		0.60	0.53

* *N* denotes the number of specimens in each sample; *S.D.* is the standard deviation.

all cases measured at the base of the enamel at the widest part of the tooth (usually the anterior pair of columns in the molars); "height" is maximum height of enamel, measured on the buccal side in upper teeth and on the lingual side in lower teeth. In canines measurements are made at the alveolar margin (except where otherwise stated); the least diameter is found first and the maximum is measured at right angles to it (in lower teeth these are, respectively, the posterior face and the anteroposterior dimension). In incisors, "length" is transverse, parallel to the edge of the premaxillae, and "breadth" is anteroposterior; "height" is height of enamel above roots on the anterior face along the axis of elongation of the tooth.

Upper Incisors

The upper incisors are preserved only in the holotype specimen and have been described fully in the account of that specimen. The dimensions are given in Table 4.

Upper Canines

The upper canines are intact only in the holotype and the subadult skull, but in

TABLE 4. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF UPPER INCISORS

Specimen No. (KP)	Tooth	Transverse (length)	Antero-posterior (breadth)	Height
239	RI^1	19.5	11.5	11.0+
	RI^2	21.2	8.5	9.0+
	RI^3 alveolus	(14.0)	(9.5)	–

TABLE 5. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF UPPER CANINES

Specimen No. (KP)	Position	Maximum	Minimum	Length
239	left	22 m	16 m	37+b
	right	20 m	17 m	39+b
264	left	34 a	25	–

a – within alveolus
m – at margin of alveolus
b – from margin of boss

TABLE 6. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF UPPER P^2

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
244		Very slight	12.0	6.7	6.0
239	left	Slight	11.2	7.0	6.2
	right	Slight	11.6	6.8	6.5
201		Moderate	12.6	7.4	(6+)
264		Moderate	13.2	8.9	8.0
Mean			12.1	7.4	
Standard Deviation (S.D.)			0.711	0.806	

the paratype the cross section of the root can be seen. Its flattened oval shape is unlike that seen in any living form. The canines of the female have enamel only at the tips and resemble those from Olduvai Bed I which have closed or nearly closed roots; there can be no doubt that the same is true for the tusks of the holotype. The cross section of the broken canine in the paratype shows a great thickness of dentine, absence of enamel, and a very small pulp cavity. Measurements are given in Table 5.

Upper Premolars

P^2 of both sides is preserved in the holotype, the right P^2 in the paratype and in the broken maxilla (KP 201), and the left P^2 in the subadult skull. Measurements are given in Table 6. This tooth is small and oval or subtriangular in outline, with a stout cusp anteriorly and behind it a cusp of almost equal height on a broad and pustulate cingulum. A cingular ridge extends along the lingual side and partly encloses a long and narrow fovea.

P^3 is a robust tooth of subtriangular shape, broadest at the back. There is a very strong main cone that is divided near the top into two cusps (paracone and metacone). From the anterior crest, a steep shallow ridge runs to the anterointernal border, where there is a small cingulum and weak cingular cusp. A corresponding ridge runs diagonally backwards to the posteroexternal corner and meets a high, slender cingulum cusp. The main cone forms the full width of the crown anteriorly but at the posterointernal corner there is a well-developed cusp extending about half the height of the main cone. The essential structure is rather like that of *Potamochoerus*, but the main cone is much stouter and the major axis runs more diagonally across the crown. Measurements are given in Table 7.

TABLE 7. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF UPPER P^3

Specimen No. (KP)		Stage of Wear	Length	Breadth	Height
227		Almost unworn	(26.8e)	20.5	(c22)
244		Almost unworn	20.2	(21.4e)	26.6
239	left	Moderate	22.7	18.6	18.2+
"	right	Moderate	23.5	18.5	18.5+
201		Heavy	23.8	19.2	13.5+
264		Extremely heavy	24.9	20.8	5.0+
Mean			23.7	19.8	
S.D.			2.013	1.126	

Table 8. *Nyanzachoerus pattersoni* dimensions of upper P^4

Specimen No. (KP)		Stage of Wear	Length	Breadth	Height
244		Almost unworn	20.1	23.5	27.0
227		Very slight	20.3	24.2	21.5
223		Slight	19.4	21.8	17.9+
239	left	Moderate	18.2	21.1	15.0+
"	right	Moderate	18.0	21.0	13.5+
201		Heavy	18.0	22.5	11.5+
264		Extremely heavy	19.8	(c23)	5.0+
Mean			19.1	22.4	
S.D.			0.950	1.187	

P^4 is essentially like that of *Potamochoerus* but enlarged and relatively much higher crowned. There is a strong double outer cone (paracone and metacone) the crests of which are much less separated than in *Potamochoerus*. On the lingual side lies another cone (protocone) which, although smaller than the main buccal cones, rises to the same height. Spurs from the two buccal crests project towards the lingual cusp, leaving a central fovea or narrow longitudinal cleft. Anterior and posterior cingula rise to two-thirds the height of the main cusps and fuse with the flanks of the lingual cone but do not "wrap around" it as they do in *Potamochoerus*. With moderate wear, as in the holotype, a large single island develops from the paracone and metacone, and on the lingual side there is a smaller enamel island developed from the protocone. The pustules or conelets on the cingulum seem to be composed only of enamel, and wear does not result in exposure of any dentine. Although essentially like the corresponding tooth of *Potamochoerus* in structure, there is also a slight resemblance to the upper fourth premolars in the Indian forms *Conohyus* and *Sivachoerus*—but in these genera P^4 has an inner cingulum not present in either *Potamochoerus* or *Nyanzachoerus*. In *Potamochoerus* P^4 is narrower than M^1 and no more than two thirds as broad as M^2; in *Nyanzachoerus* P^4 is broader than M^1 and about 90 per cent as broad as M^2. Dimensions for P^4 are given in Table 8.

The Upper Molars

As has been stated above, in general structure the molars are very like those of *Potamochoerus* except for the slightly

Table 9. *Nyanzachoerus pattersoni* dimensions of upper M^1

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
227		Moderate	22.5	–	7.0+
244	left	Moderate	23.0	19.2	9.5+
"	right		22.8	20.1	10.5+
239	left	Heavy	19.3	18.3	0.5+
"	right		18.5	17.3	1.0+
201		Heavy	20.8	19.3	3.5+
264		Heavy	21.2	–	–
Mean			21.2	18.8	
S.D.			1.629	0.958	

TABLE 10. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF UPPER M^2

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
205		Unerupted	29.6	23.7	22.0
227		Slight	31.8	28.4	20.7
244	left	Early	31.7	24.6	19 +
"	right		32.0	24.8	19 +
239	left	Moderate	29.8	25.5	8 +
"	right		27.5	24.1	10 +
201		Moderate	30.7	23.8	12.5+
264	left	Extremely heavy	26.3	(24e)	5 +
"	right		26.3	(24e)	5 +
Mean			29.7	24.9	
S.D.			2.006	1.421	

greater hypsodonty and the more decided separation of the main paired pillars (Pls. 5, 7). Because of its early eruption, M^1 quickly becomes a featureless tract of dentine, but fairly early wear stages are shown in the subadult skull (KP 244) and in a fragmentary immature skull (KP 227). It has the usual "five-spot" arrangement with an anterior and a posterior pair of columns and a median column between them. Small accessory cusps lie between the main columns on the lingual side. The front and back have well-developed cingula, the anterior one running almost the width of the tooth. The second upper molar is simply an enlarged version of the first molar. With advancing wear both these teeth tend to become broader and, as the cingula are worn, also shorter. The breadth across the anterior pair of pillars is only a trifle less than that across the posterior pair.

The third molar is a subtriangular tooth, distorted so that the buccal length is greater than the lingual. There is an anterior cingulum like that in the first and second molars together with an enlarged talon. A median column separates the first and second pair of pillars and another lies between the second pair and the talon. The columns of the talon tend to form a continuation of the "2 + 1" cusp pattern on the crown of the tooth, with a pair of lateral pillars (of which the lingual is the larger) followed by a posterior one. There is, however, some variation in the degree of de-

TABLE 11. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF UPPER M^3

Specimen No. (KP)		Stage of wear	Length	Breadth		Height	
				Anterior	Talon	Anterior	Maximum
223	left	Early	51.4	30.7	21.4	18+	19.5
"	right		49.0	(30e)	21.0	17+	(20+)
239	left	Moderate	48.7	32.2	18.7	18.5+	20+
"	right		48.5	31.4	18.6	17+	18+
201		Moderate	50.0	28.8	19.8	19+	21
264	left	Very advanced	51.6	31.8	20.0	10+	16+
"	right		49.1	32.4	21.0	11+	19+
Mean			49.8	31.2	20.1		
S.D.			1.192	1.231			

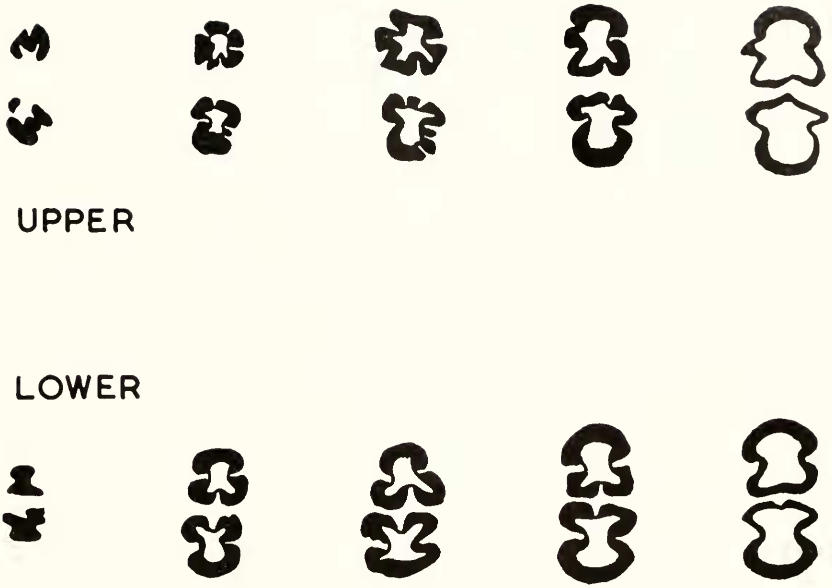

Figure 6. Generalized reconstruction of a pair of lateral columns in upper and lower molars of *Nyanzachoerus pattersoni* to show changes in the form of the enamel islands with increasing wear. The lingual side is at the top of the drawing. Approximately nat. size.

velopment of these talon cusps; the buccal and posterior pillars may be so small that the larger lingual pillar becomes effectively a posterior pillar.

The pattern of the enamel islands in the molar teeth with advancing wear is similar to that found in *Potamochoerus*, but the dentine areas are relatively larger and so the pattern is more obvious. The columns are not simple cones that wear to expose a circular core of dentine but are vertically grooved so that the enamel is infolded. The buccal columns are essentially bilobed, the buccal segment being transversely elongated, while the inner segment is axially longer and initially trilobate. The lingual columns are stellate rather than bilobate. As wear proceeds, the buccal enamel islands first assume a bell-shaped outline, while the lingual ones remain five rayed, but later the lingual element becomes progressively more rounded and like the buccal column. Figure 6 indicates the appearance of the enamel islands in their various stages of attrition. The cheek teeth of the holotype are illustrated in Plate 5. Measurements of the upper molars are given in Tables 9–11.

Table 12 gives measurements for the overall lengths of the premolar and molar series and the ratios between them. The average ratio in the uppers is .57 compared with about .53 in *Potamochoerus*. The difference is almost entirely accounted for by the relatively greater length of the third premolar in the fossil. Table 13 shows the lengths of the individual teeth expressed as percentages of the overall length of the premolar/molar series: the proportional enlargement of the third premolar is obvious. Table 14 compares the maximum breadth of each tooth with the breadth of the second molar, which is a convenient standard for comparative purposes. Length/breadth ratios have already been given in Table 3.

Upper Milk Dentition

Only one small fragment of a juvenile right maxilla is preserved (KP 222). It

Table 12. *Nyanzachoerus pattersoni* lengths of premolar and molar series

Specimen No. (KP)		Stage of Wear	P^2–P^4	M^1–M^3	P^2–M^3	P^2–P^4 / M^1–M^3
		Upper Dentition				
244	left	Very early (subadult)	49.8	–	–	
〃	right		49.5	–	–	
225		Early (adult)	–	102.0	–	
239	left	Early to moderate	51.9	95.2	147.0	.54
〃	right		51.6	94.5	146.0	.55
201		Moderate	50.5	101.5	152.0	.49
264	left	Very advanced	68.0	99.1	(162e)	.69
〃	right		68.0	96.0	161.6	.71
Mean			55.6	98.1	153.7	.60
S.D.			7.876	2.987	6.904	

Specimen No. (KP)		Stage of Wear	P_2–P_4	M_1–M_3	P_2–M_3	P_2–P_4 / M_1–M_3
		Lower Dentition				
213		Very early	(52e)	97.9	(150e)	(.53e)
256		Early	–	106.4	–	–
239	left	Early to moderate	57.4	94.0	151.4	.61
〃	right		55.5	94.5	153.0	.59
263		Moderate	(54e)	97.0	(151e)	(.56e)
240		Moderate	(c57)	(c96)	(c153)	(c.60)
258		Moderate	–	(c99)	–	–
264		Moderately advanced	69	105	174	.66
219	left	Very advanced	62.1	102.7	164.8	.58
〃	right		63.3	102.4	165.7	.62
Mean			59.8	100.0	158.6	.59
S.D.			5.567	4.462	8.793	

Table 13. Length of each cheek tooth as a percentage of length of the series P2–M3 in *Potamochoerus* and *Nyanzachoerus*

UPPER DENTITIONS	P^2	P^3	P^4	M^1	M^2	M^3
Potamochoerus porcus	9.5	12.6	12.4	16.2	21.0	28.3
Nyanzachoerus pattersoni	7.8	15.3	12.3	13.6	19.1	32.0
N. tulotos	10.0	16.2	13.2	14.8	18.9	26.9
N. plicatus	6.1	13.1	10.6	10.6	20.5	39.1

LOWER DENTITIONS	P_2	P_3	P_4	M_1	M_2	M_3
Potamochoerus porcus	5.3	10.8	14.1	14.9	21.7	33.2
Nyanzachoerus kanamensis	6.0	17.2	13.0	15.0	18.6	30.2
N. pattersoni	6.6	16.0	14.0	12.5	16.9	34.0
N. tulotos	9.6	17.6	15.5	13.0	17.4	26.9
N. plicatus	5.7	13.1	12.2	10.8	18.2	40.0

TABLE 14. BREADTH OF EACH CHEEK TOOTH AS A PERCENTAGE OF THE BREADTH OF THE SECOND MOLAR IN *POTAMOCHOERUS* AND *NYANZACHOERUS*

UPPER DENTITIONS	P^2	P^3	P^4	M^1	M^2	M^3
Potamochoerus porcus	31	50	64	78	100	100
Nyanzachoerus pattersoni	29	78	89	75	100	124
N. tulotos	38	81	95	77	100	100
N. plicatus	25	69	76	c72	100	126

LOWER DENTITIONS	P_2	P_3	P_4	M_1	M_2	M_3
Potamochoerus porcus	30	45	60	74	100	100
Nyanzachoerus kanamensis	30	75	83	c74	100	109
N. pattersoni	34	97	96	69	100	120
N. tulotos	38	97	99	76	100	108
N. plicatus	38	89	90	90	100	125

consists of the dm^4 in fairly advanced wear, and the anterior two-thirds of the M^1. This specimen occludes well with the portion of juvenile mandible KP 221, and could well have come from the same individual. The unerupted large P^4 can be seen in the alveolus below the dm^4. The milk molar is essentially similar to that of *Potamochoerus* of approximately the same dental age, although the tooth in the fossil is somewhat longer as a result of the slight enlargement of the posterior cingulum. The permanent M^1 in the fossil is typical of *Nyanzachoerus*. The measurements are given in Table 15.

The Lower Dentition

The lower dentition is not complete in any of the specimens but the relationships of the teeth are best seen in the mandible of the holotype (Pl. 2). The cheek teeth are damaged in the mandible of the holotype and badly damaged in that of the paratype; they are present in the mandible of an old individual (KP 219), but the canine area is badly damaged and the incisors are lost. In the holotype there is a diastema of 48 mm between the front of the root of P_2 and the back of the canine; the distance from P_2 to the back of I_2 is 72 mm; the lower canine is intact and there is no diastema between it and I_3. The canines are broken in the mandibles of the paratype and of the old individual but one is present in a juvenile jaw in which the premolars are unerupted (KP 266). The milk molars occur in fragments of a pair of mandibular rami (KP 221) and the milk incisors are also present, but the canine-bearing area of the jaw is missing. Cheek teeth are preserved in several other incomplete mandibular rami. Table 16 gives the observed ranges of size and average measurements.

TABLE 15. DIMENSIONS OF JUVENILE UPPER TEETH IN *NYANZACHOERUS PATTERSONI* AND *POTAMOCHOERUS*

				Height	
		Length	Breadth	Anterior	Posterior
Potamochoerus	dm^4	13.5	11.5	5 +	4.5+
KP 221	"	15.5	12.4	5.5+	5.5+
Potamochoerus	M^1	16	12.5	8.5+	8 +
KP 221	"	15.5+ (20e)	16	12.5+	–

TABLE 16. AVERAGE DIMENSIONS OF LOWER CHEEK TEETH OF *NYANZACHOERUS PATTERSONI* COMPARED WITH *N. KANAMENSIS*

		N. pattersoni			*N. kanamensis*		
		Range	*N**	S.D.*	Mean	Holotype	Paratype
P_2	length (L)	10.4 – 10.7	2		10.6	c10	
	breadth (B)	7.2	2		7.2	c 6	
	L/B	1.45– 1.48			1.47	c 1.6	
P_3	length	24.0 – 27.1	4	1.279	25.7	28.9	
	breadth	19.3 – 21.7	4	0.960	20.3	15.1	
	L/B	1.24– 1.30			1.26	1.91	
P_4	length	21.0 – 23.4	6	0.800	22.5	21.6	
	breadth	18.9 – 21.8	6	1.284	20.5	16.8	
	L/B	1.07– 1.19			1.11	1.29	
M_1	length	18.3 – 21.9	8	1.193	20.2	c25	
	breadth	13.2 – 16.5	7	0.953	14.2	c15	
	L/B	1.10– 1.58			1.39	c 1.7	
M_2	length	24.5 – 29.7	11	1.262	27.6	31.0	28.0
	breadth	17.7 – 22.8	10	1.537	21.1	20.2	19.7
	L/B	1.19– 1.39			1.32	1.53	1.42
M_3	length	49.6 – 59.2	13	2.785	54.7	50.5	51.0
	breadth	22.8 – 28.6	11	1.801	25.1	22.0	23.2
	L/B	1.97– 2.35			2.17	2.28	2.24
$P_2 - P_4$		52.1 – 69.0	7	5.567	59.0	c60.5	
$M_1 - M_3$		94.0 –106.4	8	4.462	100.0	106.5	
$P_2 - M_3$		150.0 –174.0	7	8.793	158.6	167.0	
$\frac{P_2 - P_4}{M_1 - M_3}$		0.53 – 0.66	7		0.59	0.56	

* *N* denotes the number of specimens in the sample; S.D. is the standard deviation

As is the case with the upper cheek teeth, the lowers are structurally very similar to those of *Potamochoerus* and likewise differ mainly in the more columnar nature of the paired pillars in the molars and in the greater hypsodonty and enlargement of the premolars (Pls. 6, 8, 9). In *Potamochoerus* the third molar normally terminates in a pair of pillars that may be poorly developed or may be almost as well developed as the second pair, but only rarely is there a median pillar at the back of the tooth. In *Nyanzachoerus* the third pair of pillars is well developed and there is a terminal median pillar on the talonid.

Lower Incisors

The lower incisors are preserved only in the mandible of the holotype and have been described fully in the account of that specimen. The measurements are given in Table 17.

Lower Canines

There is a substantial size difference in the canines of the sexes and they also differ slightly in shape. The female canines are fully developed in the holotype mandible, and the left canine can be seen in the alveolus in the incomplete mandible KP 240; an isolated tip of a right canine (KP 224) matches that of the holotype. The cross section is almost heart-shaped near the base, becoming more triangular towards the tip. The back of the tooth has a broad shallow groove that disappears as the surface becomes flattened by attrition. The wear facet is oriented in the vertical plane, as it is in *Hylochoerus*, but does not show the slight backward slope from the dorsal to the ventral edge that is seen in *Phacochoerus*. The male canines, seen broken off in the paratype mandible and in the old mandible KP 219, are similar in cross section shape but 50 per cent larger. The respective cross sections are illustrated, natural size, in Figure 5 and the dimensions are given in Table 18. The posterior face is free of enamel, but the two lateral faces are covered with thin enamel, weakly grooved longitudinally, and with fine transverse striations that give a reticulate appearance to the enamel; it may be remarked that this finely reticulate enamel is also observed in the incisors and cheek teeth and is therefore of assistance in the diagnosis of teeth of *Nyanzachoerus*. The canines of the male are directed somewhat more laterally than those of the female and they were probably 10–15 cm long beyond the jawbone. The lower canines in the male appear to have open roots, whereas those of the female seem to be partly closed.

TABLE 17. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF LOWER INCISORS

	I_1	I_2	I_3
Holotype skull KP 239			
Transverse (length)	9.2	11.1	11.2
Anteroposterior (breadth)	11.6	11.4	9.6
Height	18.6	25.0	15.0+

The Premolars

P_2 is preserved complete in the holotype, and somewhat worn in the male jaw KP 219. By contrast with the enlarged premolar behind it, it is a rather small tooth consisting of a low stout cone with a distinct posterior ridge, a small secondary posterior cusp, and a poorly developed cingulum. *Potamochoerus* normally has simpler and narrower teeth, comprising a single cone only, though a posterior cusp is sometimes present, together with anterior and posterior cingula.

P_3 is a robust tooth with a strong main cone (protoconid) and a moderately strong posterior cingulum with a small posterior cone rising from it; the cingulum and its cone rise one-half to two-thirds the height of the main cone. The tip of the main cone is centred over the front part of the posterior root, giving the cone an asymmetrical profile with a backward slant. This is even more marked in the longer and narrower P_3 of *N. kanamensis*. In the latter species there is also a very small anterior cusp that has not been observed in the specimens of *N. pattersoni*, although there is a very weak anterior cingulum in both species. Measurements are given in Table 20.

P_4 is also a stout tooth, with a conical protoconid, well-developed posterior cingulum and a posterior cusp three-quarters the height of the main cone. There is also a less massive anterior cingulum rising almost to half the height of the main cone. The protoconid is ridged anteriorly and posteriorly, the ridge lying slightly towards the lingual side of the centre line. In *N. kanamensis* the anterior cingulum is a little weaker and the whole tooth is proportion-

TABLE 18. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF LOWER CANINES

Specimen No. (KP)	Position measured	Maximum	Minimum	Length
239 left	At alveolus border	21	12.7	45.0+
" right	At alveolus border	23	13.4	45.5+
240	Within alveolus	21.7	15.7	–
264 left	Within alveolus	33.7	24.9	–
" right	Within alveolus	34.7	24.7	–
219	Within alveolus	31.0	22.0	–

Table 19. *Nyanzachoerus pattersoni* dimensions of lower P_2

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
239		Roots only	(c10)	(c8.5)	–
263		Socket	(c 6)	–	–
219	left	Moderate	10.7	7.2	6.5+
″	right	Moderate	10.4	7.2	6.5+

ally narrower than in *N. pattersoni.* The posterior foveae are more distinct in *N. kanamensis* than in *N. pattersoni.* Measurements are given in Table 21.

The Lower Molars

The molars are structurally very like those of *Potamochoerus,* but the cusps are more distinctly columnar and there is relatively more dentine in the enamel islands. In most of the specimens M_1 is worn to dentine, but the pattern can be clearly seen in two specimens that have milk teeth (KP 221 and 266) and also in the left mandible KP 213, in which M_3 is still in the process of eruption. Both M_1 and M_2 have two pairs of lateral pillars, a single median column, and anterior and posterior cingula. M_3 has three pairs of lateral pillars, separated by single median columns and a stout talonid pillar at the back. In the mandible KP 256 the back of the talonid has two smaller terminal pillars and a very small median pillar, forming an incipient extra pair of laterals. Several of the teeth have a small basal pillar on the

Table 20. *Nyanzachoerus pattersoni* dimensions of lower P_3

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
213		Almost unworn	24.0	19.3	25.2
239		Roots only	(23.5e)	(16.0e)	
263		Early	25.0	19.5	18.7+
219	left	Well worn	27.1	21.7	19.4+
″	right		26.8	20.6	15.5+
Mean			25.7	20.3	
S.D.			1.279	0.960	

Table 21. *Nyanzachoerus pattersoni* dimensions of lower P_4

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
213		Very early	21.0	19.1	22.0
255		Moderate	22.4	22	(14.5e)
256		Moderate	22.7	19.9	17.5+
239		Root only	(c20.5)	(c16)	–
263		Moderate	22.4	18.9	19.0+
219	left	Very advanced	23.4	21.8	6.5+
″	right		23.3	21.5	5.5+
Mean			22.5	20.5	
S.D.			0.800	1.284	

TABLE 22. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF LOWER M_1

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
221	left	Just beginning	21.5	13.9	14
"	right		21.9	13.9	14.5
228		Very slight	19.3	13.9	15.1
205		Slight	19.8	13.5	11.5+
266		Moderate	20.9	13.2	3.5+
213		Advanced	20.6	15.3	8.0+
263		Extreme	18.3	16.0	d
219		Extreme	19.0	(16.5e)	d
Mean			20.2	14.2	
S.D.			1.193	0.953	

lingual side of the talonid, and there is also a tendency for two or three small basal pillars to develop between the pairs of lateral columns. The anterior cingulum is thin but extends more than half the height of the anterior pair of pillars. Measurements are given in Tables 22–24. The lateral pillars are divided by three grooves, an axial one that is relatively weak and a stronger anterior and posterior pair. As a result, they wear into a complex trilobed pattern, consisting of an individual outer lobe, clearly separated off from a double inner lobe. With advancing wear, the outer lobe elongates so that in moderately advanced wear the lateral element is approximately the same length as the double inner lobe length and its shape becomes rather bell-like. The stages are illustrated in Figure 6 and actual examples are seen in Plate 5.

The Lower Milk Dentition

Two specimens, KP 221 and 266, display some of the milk dentition and have the first molars preserved so that assignment to the species is not in doubt, and they also possess the characteristic enamel. The more juvenile is KP 221, which consists of several pieces of mandible and two small skull fragments. The mandibular remains comprise the front of the symphysis with five

TABLE 23. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF LOWER M_2

Specimen No. (KP)		Stage of wear	Length	Breadth	Height
220		Early	27.7	21.1	19.0+
266		Early	28.3	17.7	16.5+
213		Moderately early	28.2	20.2	15.1+
260		Moderate	26.8	20.2	
255		Moderate	29.7	22.8	10.5+
256		Moderate	28.7	21.4	10.4+
239		Root only	(c25)	(c18)	
263		Advanced	28.0	21.8	7.5+
240		Advanced	27.2	20.2	8.5+
219	left	Extreme	27.8	(23e)	2 +
"	right		27.1	22.7	3 +
259		Extreme	24.5	(c24)	d
Mean			27.6	21.1	11.5+
S.D.			1.262	1.537	

TABLE 24. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF LOWER M_3

Specimen No. (KP)	Stage of wear	Length	Breadth		Height	
			Anterior	Talon	Anterior	Maximum
213	Incompletely erupted	49.6	(22.5e)	–	19.2	23
256	Early	59.2	25.1	20.7	17+	19
239 left	Moderately early	53.6	22.8	20.0	18+	18.5+
″ right		52.9	22.8	20.2	17.5+	18+
263	Moderate	50.3	24.8	20.2	12.3+	13.5
240 left	Moderate	55.0	24.0	18.6	11+	12.5+
″ right		54.2	23.8	18.3	10+	12.5+
258	Moderate	52.7	25.1	20.1	13.5+	15.0+
264 left	Moderate	56.2	26.3	21.4	11.5+	13.5+
″ right		58.5	(26+)	22.9	14.0+	14.5+
219 left	Very advanced	56.4	28.6	22.7	3+	4.5+
″ right		57.0	27.9	22.5	4.5+	6+
259	Extreme	55.2	24.7	20.8	5	5+
Mean		54.7	25.1	20.7		
S.D.		2.785	1.801			

incisors; portions of mandibular rami containing the left dm$_{2-4}$ and M$_1$ and the right dm$_{3-4}$ and M$_1$, together with two small pieces of the lower border of the angle of the jaw. The first and second incisors are very similar in structure to those of *Potamochoerus* of similar age but a good deal longer; dI$_3$ in the fossil is a small distorted peg and is clearly not normal. The milk molars are structurally similar to those of *Potomachoerus* but are larger. However, dm$_2$ is as long as dm$_3$ and about twice as long as the dm$_2$ in *Potamochoerus;* it is astonishingly like a miniature of the adult P$_3$. Dm$_2$ is slightly broader than dm$_3$. Comparative measurements are given in Table 25 and the milk teeth are shown in Plate 11. In a *Hylochoerus* skull of comparable dental age, the angle of the mandible already shows the characteristic broadened border. In the fossil fragments, as in the adult specimens already described, this broadening is absent and the margin is no wider than the body of the bone.

Specimen KP 266 is part of a left mandibular ramus broken anteriorly and exposing the young permanent canine in early growth; the jaw is broken behind the partly worn M$_2$. At this early stage of development the posterior face of the canine is very slightly convex and lacks the groove characteristic of more mature tusks. In other respects it resembles the adult tusks. The dm$_3$ and dm$_4$ have been lost *post mortem* but the worn remnant of dm$_2$ is still in position. The tips of the main cone and cingulum crest of the permanent P$_4$ are emerging from the crypt. M$_1$ is in fairly advanced wear and M$_2$ in moderately early wear. The permanent teeth are very characteristic and make identification certain.

Postcranial Material

The vertebrae associated with the holotype have been described above. In addition there is a group of limb bones, numbered KP 215, which was found with tooth fragments sufficient to identify the species as *N. pattersoni.* This collection includes a left tibia, left fourth metatarsal, and some phalanges. Two other bones, numbered KP 243, are, respectively, a right tibia and a right third metatarsal of similar size and character, which may also be regarded as belonging to the same species. However, in the account that follows

TABLE 25. *NYANZACHOERUS PATTERSONI* DIMENSIONS OF LOWER MILK DENTITION

		KP 221		KP 266	Juvenile *Potamochoerus*
		left	right		
dI_1	Transverse	4.3	4.3	–	3.5
	Anteroposterior	4.6	4.6	–	4.0
	Height	8.5+	8.5+	–	9.5
dI_2	Transverse	5.6	5.2	–	4.4
	Anteroposterior	5.3	5.5	–	5.3
	Height	14.0+	13.5+	–	13.0
dI_3	Transverse	–	2.7	–	2.8
	Anteroposterior	–	2.9	–	2.8
	Height	–	2.0	–	4.0
C	Maximum	–	–	13.0	–
	Minimum	–	–	7.0	–
dm_2	Length	10.4	–	10.4	6.7
	Breadth	6.4	–	5.2	3.3
	Height	9.5+	–	4.5+	4.7+
dm_3	Length	10.4	10.4		9.8
	Breadth	6.2	6.2		5.1
	Height	8.0+	8.0		8.2+
				gap 28.0	
dm_4	Length	22.2	21.9		20.4
	Breadth	10.3	10.2		9.0
	Height	5.0+	4.0+		6.8+
M_1	Length	21.5	21.9	20.9	18.2
	Breadth	13.9	19.9	13.2	11.2
	Height	14	14.5	3.5+	9.8
M_2	Length	–	–	28.3	–
	Breadth	–	–	17.7	–
	Height	–	–	16.5	–

only the associated material from KP 215 will be discussed. Measurements are given in Tables 26 and 27 and the specimens are shown in Plate 12.

Tibia

The tibia is very slightly larger than that of an average adult *Hylochoerus* female and could be matched fairly closely in an adult male. The morphology is also very similar in detail. The tuberosity at the upper part of the crest is proportionately not quite as broad as in *Hylochoerus*, and the groove for the middle patellar ligament is a little deeper, although not as deep as in *Potamochoerus* and *Phacochoerus*. The sulcus between the tuberosity and the lateral condyle is very like that of *Hylochoerus* in being wide and open laterally, whereas in both *Potamochoerus* and *Phacochoerus* the sulcus is narrowed by an anterior extension of the lateral condyle. The distal end is slightly broader across the malleoli than is the case in the three living species, both by comparison with the anterior-posterior dimension and also relative to the breadth across the proximal condyles; however, the differences are very slight. This widening of the distal end is not accompanied by a greater robustness of the shaft, for the medial/lateral dimen-

Table 26. Measurements on limb bones of *Nyanzachoerus pattersoni* (KP 215) compared with those of living African Suidae

Actual measurements in mm

	Nyanzachoerus	*Hylochoerus*	*Phacochoerus*	*Potamochoerus*
TIBIA				
length	238.0	221.0	204.0	173.0
proximal breadth	65.5	65.0	51.7	49.4
distal breadth	40.4	37.3	30.3	29.0
TALUS				
length	55.5	51.8	40.5	40.8
breadth—proximal	33.4	31.9	22.8	22.9
—distal	32.8	32.7	23.8	23.2
CALCANEUM				
length	108.0	102.1	78.8	76.0
breadth at sustentaculum	26.7	26.7	21.2	18.2
a/p diameter at sustentaculum	26.6	27.9	22.1	22.1
METATARSAL IV				
length	105.0	82.7	84.8	71.9
shaft breadth	19.7	20.6	14.9	13.1
shaft thickness (a/p)	14.0	13.7	10.7	10.4
PHALANGES—PES				
III P_1 length	46.6	42.8	37.3	32.3
prox. breadth	25.8	20.2	16.9	15.0
IV P_1 length	46.5	42.5	37.1	31.9
prox. breadth	24.3	20.5	16.6	15.3
V P_1 length	31.4	25.6	22.6	20.5
prox. breadth	14.6	13.8	10.1	9.8
PHALANGES—MANUS				
III P_1 length	44.1	43.2	37.1	31.7
prox. breadth	26.7	22.2	16.7	15.0
III P_2 length	33.1	32.4	22.7	21.1
prox. breadth	24.7	21.7	15.7	16.6
IV P_2 length	30.4	32.5	22.2	20.9
prox. breadth	25.4	21.1	15.7	14.7
IV P_3 length	35.5	33.6	25.5	26.3
prox. breadth	25.3	23.3	18.4	15.9

sions of the shaft, as compared with the overall length of the tibia, have the same proportion as in the bushpig and warthog and the bone is thus not quite as stout as in *Hylochoerus*.

Tarsal Bones

Articulating with the left tibia are the left talus, calcaneum, cuboid, and navicular.

The talus is somewhat larger than that of the forest hog and slightly more elongated. It is, however, not as narrow as in *Phacochoerus* or *Potamochoerus*, and its proportions are intermediate between those of the forest hog and the two other extant species.

The cuboid is a little damaged. It is more compressed than in the bushpig or warthog, but not as much so as in the forest hog, its morphology being intermediate between *Potamochoerus* and *Hylo-*

TABLE 27. RELATIVE PROPORTIONS OF LIMB BONES OF *NYANZACHOERUS PATTERSONI* (KP 215) AND THOSE OF LIVING AFRICAN SUIDAE

Proportions calculated relative to the length of the tibia as 100

	Nyanzachoerus	*Hylochoerus*	*Phacochoerus*	*Potamochoerus*
TIBIA				
length	100.	100.	100.	100.
proximal breadth	27.5	29.3	25.3	27.6
distal breadth	16.9	16.9	14.7	16.8
TALUS				
length	23.3	23.3	19.8	23.4
breadth—proximal	14.0	14.4	11.2	13.2
—distal	13.7	14.7	11.7	13.4
CALCANEUM				
length	45.2	46.1	38.6	43.9
breadth at sustentaculum	11.2	12.2	10.4	10.5
a/p diameter at sustentaculum	11.2	12.6	10.8	12.8
METATARSAL IV				
length	44.0	32.3	41.6	41.5
shaft breadth	8.3	9.3	7.3	7.6
shaft thickness (a/p)	5.9	6.2	5.2	6.0
PHALANGES—PES				
III P_1 length	19.6	19.3	18.3	18.7
prox. breadth	11.3	9.1	8.3	8.6
IV P_1 length	19.5	19.2	18.2	18.4
prox. breadth	10.2	9.2	8.1	8.8
V P_1 length	13.2	11.6	11.1	11.8
prox. breadth	6.1	6.2	4.9	5.7
PHALANGES—MANUS				
III P_1 length	18.7	19.5	18.2	18.4
prox. breadth	10.4	10.0	8.2	8.7
III P_2 length	13.9	14.6	11.1	12.2
prox. breadth	10.3	10.2	7.7	9.6
IV P_2 length	12.8	14.7	10.8	12.1
prox. breadth	10.7	9.5	7.7	8.5
IV P_3 length	14.9	15.2	12.4	15.2
prox. breadth	10.6	10.5	9.0	9.2

choerus in most of the details that can be seen. The navicular is also less compressed than in the forest hog and differs slightly in the size, shape, and angle of the lower facets; that for the external cuneiform is nearly equidimensional, as in the warthog. Otherwise the morphology is closest to that of *Hylochoerus*.

The calcaneum is longer than that of *Hylochoerus* but less robust so that its proportions are more like those of the bushpig. The articular facet on the lower surface of the sustentaculum is fairly smooth, as in *Potamochoerus*, but is rather wider and more equidimensional than in any of the living forms.

Other Bones of the Pes

The foot is represented by seven bones. The distal end of a left third metatarsal articulates with the first (proximal) phalanx; the left fourth metatarsal articulates with its first phalanx; and the distal end of the left fifth metatarsal is associated with its first phalanx. In addition there is the first phalanx of the fifth digit of the right side.

The left fourth metatarsal is 20 per cent longer than the corresponding bone in *Hylochoerus* but its shaft is not significantly stouter. The bone is thus, like that of the warthog, relatively long and slender and very different from the much stouter metatarsal of *Hylochoerus.* Another point in which it differs from the *Hylochoerus* metatarsal and resembles that of *Phacochoerus* is the ratio of width to anteroposterior thickness of the shaft: in *Hylochoerus* the shaft is rather flat, its width being approximately one and a half times its thickness, whereas in both the fossil and in *Phacochoerus* the disparity between the two diameters is rather less. The plantar projection is broken in the fossil and the general form of the proximal articular surface is otherwise *Potamochoerus*-like, but not very distinctive. There are no very characteristic features of the distal end, except that the articular facets are relatively a little wider than in the forest hog or the other living species.

The first phalanges of the third and fourth digits are differently proportioned from those of the three living species, in which the phalanges are rather similar. In length and in the dorsoventral dimensions of the proximal end of these phalanges the fossil is 10 per cent bigger than in the living *Hylochoerus;* however, the lateral-medial dimension is 20 per cent greater, so that the toes are proportionally wider (or are relatively shorter and stubbier). The first phalanges of the fifth digit, however, are proportioned like those of the bushpig and are relatively longer than the corresponding ones in the forest hog, although the differences are small.

Bones of the Manus

Of the front foot are preserved only phalanges for digits three and four of the right side. In the third digit both the first and second phalanges are intact; in the fourth digit, the first phalanx lacks the distal half, but the second and third phalanges are entire. In length they are very close to the corresponding bones in the forest hog but, as with the hind foot, the phalanges are wider, so that it would be equally true to say that they are relatively shorter or more compressed. Apart from the effect of this anteroposterior compression on the proportions, there are no significant differences that warrant comment, although *Phacochoerus* is least like the fossil phalanges in proportions. The terminal phalanx of *Potamochoerus* is decidedly narrower than that of the fossil; its articular region resembles that of *Hylochoerus.* However, the fossil phalanx has a thin "splayed out" border or flange on the anteromedial side, rather like that of *Potamochoerus.* In addition the second phalanx in digit three is relatively long, being 75 per cent of the length of the first phalanx; *Hylochoerus* gives the same ratio, whereas in *Phacochoerus* the corresponding value is only 60 per cent.

Unfortunately the material is not sufficient to give a full picture of the structure of either the fore or the hind limb of *Nyanzachoerus.* A few points of interest, however, emerge from a comparison with the extant African species. Of these *Phacochoerus* and *Hylochoerus* are of most interest. The limbs of the former show a number of cursorial adaptations: the humerus and femur are fairly short and the manus and pes rather narrow and elongated. This is shown in the narrow talus, the long slim metapodials and the proportions of the phalanges, the first being long and the second and third relatively short. In *Hylochoerus* the gait is less digitigrade and the foot broader and more spreading, in adaptation to locomotion on rather soft or even marshy ground. The proximal limb segments are long, the metapodials broad but not particularly thick anteroposteriorly and the disproportion between first and second phalanges is less.

Unfortunately no femur of *Nyanzachoerus* is known. However, the fourth metatarsal is 44 per cent of the length of the tibia, as compared with 41.6 per cent in *Phacochoerus*. It seems more reasonable to interpret this as meaning that the tibia is not particularly elongated and the femur therefore not correspondingly shortened, rather than as implying metapodials even more specialised than those of *Phacochoerus*. There is nothing in the rest of the limb bones known at present that would warrant the latter conclusion. However, even if the femur were not shortened, there are a few points in which the limbs differ from those of *Hylochoerus* and show some similarity to those of *Phacochoerus*, for instance, the elongation and narrowness of the metatarsals and the somewhat compressed tarsal bones.

Without more complete material it is difficult to draw any very positive conclusions about the limbs of *Nyanzachoerus*. It does, however, seem clear that while *Nyanzachoerus* may not have possessed such cursorial adaptations as are characteristic of *Phacochoerus*, it did not have the broad spreading hylochoerine type of foot and its limbs were not specially adapted to locomotion on soft ground.

Nyanzachoerus plicatus sp. nov.*

Text-figures 7–9; Plates 13–18

Hylochoerus Hopwood, 1931: 133.
Mesochoerus paiceae Leakey, 1958 (in part): 13.

Diagnosis. A species of *Nyanzachoerus* larger than the extant *Hylochoerus*. Third molars only slightly hypsodont; larger and more elongated than those of *N. pattersoni* and *N. kanamensis*. Upper third molars with three pairs of lateral pillars and talon pillar; length about twice breadth. Lower third molars with three pairs of lateral pillars and posterior complex; length about two and two-thirds times breadth. Premolars relatively less enlarged than those of *N. pattersoni*, with premolar series (P2–P4) approximately 40–50 per cent of the length of the molar series; P_4 about one-third the length of M_3. Enamel on molars more infolded than in *N. pattersoni* or *N. kanamensis*, giving a complex pattern to the enamel islands produced by wear, particularly in M^3. Upper canines relatively small, devoid of enamel, flattened oval in section, and forming roots very early.

Holotype. KNM–KP 251: associated partial skull and damaged mandible.

Paratypes. KNM–KP 252: three upper canine teeth found with the holotype but not belonging to it. KNM–KP 262: associated pieces of mandible and skull. KNM–KP 257: portion of skull with cheek teeth.

Locality. Kanapoi, northwestern Kenya.

Horizon. Kanapoi sediments; probably Upper Pliocene.

REFERRED SPECIMENS

KNM–KP 235: parts of mandible with LM_3, broken RP_4, and pieces of lower canines; isolated LM^3 and fragment of RM^3; parts of the pelvis; third cervical vertebra. KP 254: isolated RM_3. KP 269: two parts of mandibular rami with milk teeth. KP 203: half of upper canine. KP 206: incomplete RM^2. KP 253: isolated RM^3. KP 225: isolated, damaged RM^3, and back portion of matching LM^3.

DESCRIPTION

The Holotype Skull and Mandible

The holotype (KNM–KP 251) comprises a badly damaged partial skull, found with a damaged mandible, and also associated with a pair of canines and some canine fragments (KNM–KP 252). The fragments could belong to the skull, but sufficient of the tusks are preserved in the holotype to make it clear that the more complete canines cannot have come from the skull

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* *N. plicatus* has been referred to in several preliminary faunal lists as *Nyanzachoerus* species "B."

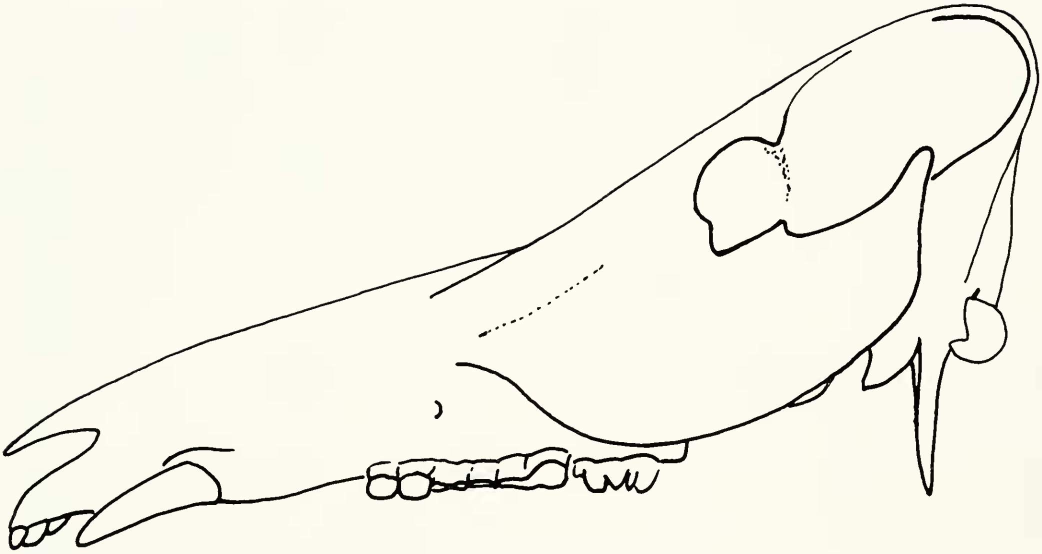

Figure 7. Attempted reconstruction of the skull of *Nyanzachoerus plicatus*. × ¼.

itself. These canines undoubtedly belong to the same species and are cited as paratypes.

The skull—if it can be dignified by such a designation—consists mainly of the snout from a point 7 cm behind the supraorbital foramina to the front of the canine fossae. The right side is very badly damaged, but the left side shows the lacrimal area and maxillary part of the beginning of the zygomatic arch (Pl. 13). A partial and very tentative restoration, based on all the material available and especially on the holotype and the third paratype, is given in Figure 7.

The lacrimal and supra-orbital foramina and a very small part of the margin of the orbit are preserved on the left side. The arrangement of the foramina is phacochoeroid; the lacrimal foramina are situated very close to the margin of the orbit and the supra-orbital foramen is virtually at the same level. In *Hylochoerus* the supra-orbital foramen lies further forward, distinctly anterior to the lacrimal foramina, and the latter lie slightly further in front of the orbit, so that the distance between the infra-orbital and supra-orbital foramina is much less than in *Phacochoerus*. This distance is no more than 10 cm in a big skull of *Hylochoerus* as against 15 cm for *Phacochoerus;* in the fossil skull, this distance is almost 20 cm, indicating that the cranium has the same sort of backward elevation as does that of *Phacochoerus*. In *Phacochoerus* this is achieved by elongation at the level of the lacrimal and jugal. In the fossil, the lower margin of the lacrimal is not complete, but the preserved portion of the suture with the jugal measures just over 5 cm in front of the orbit. In a large *Hylochoerus* the suture is no longer than 3.5 cm, so it would appear that in the fossil skull elongation has taken place in the same area as in *Phacochoerus*. In the snout region, however, the fossil skull is very different. There is no distinct preorbital constriction; the snout runs forward from the level of the infra-orbital foramen without any significant increase in width, and the nasal sutures are virtually parallel throughout their length. In this the resemblance is closer to *Hylochoerus* than to *Phacochoerus*. The contour of the snout, as it would appear in transverse section, is highly characteristic and cannot

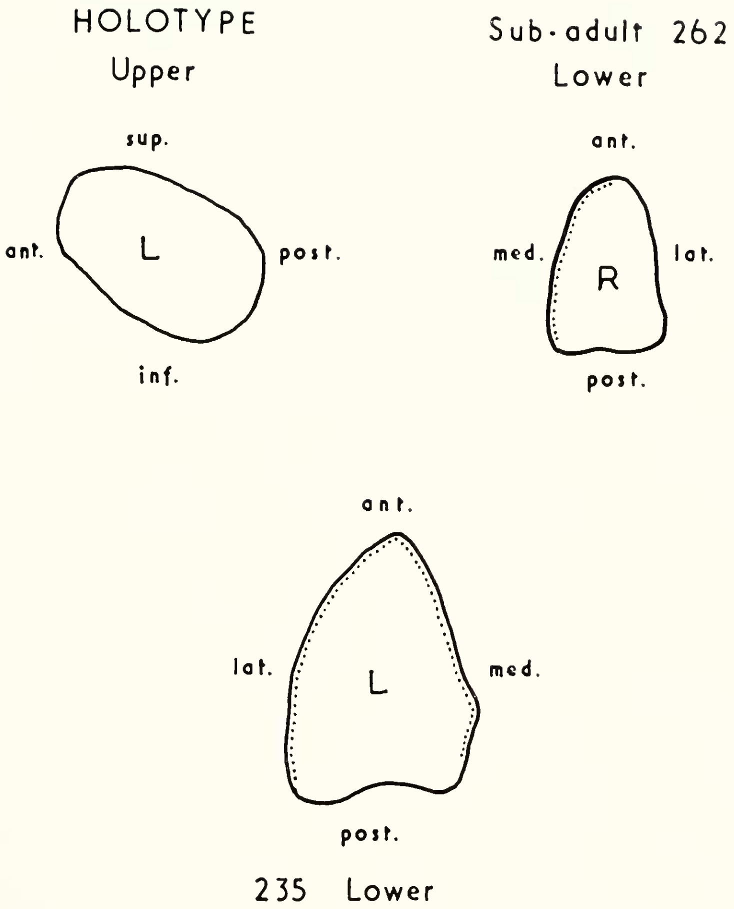

Figure 8. Sections through upper and lower canines of *Nyanzachoerus plicatus*, near the border of the alveolus. The dotted line indicates the zone covered with enamel. Nat. size. Abbreviations as in Fig. 5.

be matched in any of the extant African species. From the nasomaxillary suture ventrally, the maxillae slope inwards very slightly; at the level of the suture the bone is slightly inflated on either side to form a convex shoulder. These shoulders run backwards and would be continuous with a pair of conspicuous lateral ridges, forming the margins of the skull table just in front of the orbits, were they not interrupted in their course by the very well marked preorbital sulci passing down from the dorsal surface of the skull to the sides of the snout. The nasals, although flattened towards the midline, curve downwards then outwards to meet the "shoulders" in a smooth curve. The whole conformation of the snout is, in fact, like an elongated and narrowed version of that of *Nyanzachoerus pattersoni.*

On the sides of the snout, the flare of the zygoma starts just behind the infra-orbital foramen, but very little of it is preserved. The bony flange at the base of the canine is large but less laterally directed than in *Phacochoerus* or *Hylochoerus,* and the basal part of the canine alveolus runs almost parallel with the axis of the skull. Between the canines, the palate shows a rather more marked medial groove than

TABLE 28. MEASUREMENTS ON SKULLS OF *NYANZACHOERUS PLICATUS*

	KP 251	KP 257	KP 262
Facial length	380e		
Nasal breadth	57	c45	
Muzzle breadth	46		
Ocular breadth	130e		124
Interorbital width	116e		100e
Frontal breadth	140e		146
Bizygomatic breadth		c280–300	
Orbital height		c140–150	
Posterior platal breadth		36	
Anterior palatal breadth		53	
Postcanine breadth	c60		
Precanine breadth	c115		
Length of premolar series		left 42.5 right c46	
Length of molar series		right 116	

does that of *Hylochoerus*, flanked by ridges that are separated from the canine flanges by the usual shallow blood vessel channel.

The left canine is broken at about the original alveolar margin and its root remains in the socket; it is flattened oval in cross section, slightly narrower lingually than on the outer side, and flattened above and below (Fig. 8). The curvature indicates that the tooth emerged almost parallel to the palatal plane at an angle of about 45° to the axis of the skull. The broken cross section shows no pulp cavity. The right canine is broken well below the alveolar margin, is of similar form, and still fails to show any pulp cavity. It is thus apparent that the canines have closed roots. This is one of the important diagnostic features of the species and is possibly also a general feature of the genus *Nyanzachoerus*. A few measurements are given in Table 28.

The associated mandible has lost the incisor/canine area, the left ascending ramus, and the right ramus behind the fourth premolar, although the right third molar is preserved, embedded in an isolated fragment of alveolar bone. The front of the mandible is narrow as befits the skull; it could only have contained relatively slender canines. The symphysis was probably 120–130 mm long. In profile the outer surface of the symphysis is almost straight and its lower corner lies well below the general level of the bottom of the corpus of the mandible, which curves down to it from a point below the fourth premolar (Pl. 14). This curvature is rather more marked than in *Hylochoerus*, and the symphysis is proportionally distinctly longer. The symphysis is fairly deeply scooped out on the inner surface and laterally compressed.

The left and right third premolars are in moderately advanced wear and the third molars are in fairly advanced wear (Pl. 18). The left fourth premolar and left second molar are worn to the dentine; the left first molar is broken away and the right fourth premolar badly damaged. Some measurements are given in Table 29.

P_3. The third premolar is a stout tooth and the main cone forms the full width of the crown. There is a fairly narrow posterior cingulum with a small cingular cusp, originally perhaps two-thirds the height of the crown. There is a very small anterior cingulum cusp.

M_3. The third molar shows the existence of three pairs of lateral columns, separated by unpaired median columns and a talon complex of three or four columns. The outer walls of the paired columns are stout and broadly curved, coalescing at the base of the crown without forming a marked cingulum, but the laterals were probably well separated in the upper part of the crown. The worn surfaces of the lateral pillars have a bilobed "cottage loaf" shape, the outer lobe being larger than the axial one. The median columns are irregular in outline.

The First Paratype

From the same locality as the holotype comes a pair of complete upper canines matching exactly those of the skull; there

TABLE 29. DIMENSIONS OF LOWER CHEEK TEETH OF *NYANZACHOERUS PLICATUS*

Specimen No. (KP)	Stage of Wear	Length (L)	Breadth (B)	Height	L/B
P_2					
235	Roots	9.0	7.0	–	
P_3					
235 left	Roots	25.0	16.5	–	
″ right		21.0	16.0	–	
251 left	Moderately advanced	23.0	17.0	15.0+	1.35
″ right		23.2	16.2	15.0+	1.43
P_4					
235 left	Roots only damaged	21.5	16.5	–	
″ right		22.5	17.0	–	
251 left	Very advanced	21.4	16.7	c3+	1.28
″ right		19.0	17.0	c17	c1.12
M_1					
235 left	Roots	19.0	19.0	–	
251 left	Broken	19.0	–	–	–
M_2					
235	Roots	27.5	22.0	–	
262	Incomplete	c38	20.3	13+	c1.90
251 left	Very advanced	26	c20	–	c1.30
M_3					
254	Almost unworn	c77	29.0	30.5	2.65
262	Moderately early	c74	24.3	26.5+	3.03
235	Moderate	68.5	28.0	25.0+	2.44
Specimen KP 251					
Length of premolar series		c56	Length of molar series		112
Specimen KP 235					
Length of premolar series		c55	Length of molar series		c115

is also a small section of root of another upper canine (KNM–KP 252; Pl. 14). The canines measure respectively 159 and 155 mm from tip to root and at the widest part the maximum and minimum diameters are 31.5 × 22.0 mm and 30.9 × 21.7 mm (Table 30). The roots are completely closed. There is no enamel remaining on the teeth, even at the tips, but it is not impossible that a little enamel may have been present in the juvenile stage. Both canines show a broad wear facet on the anterior lower face. This facet truncates the curved edge of the tooth and produces a straight upper edge that would have been approximately perpendicular to the axis of the skull. As we judge from the orientation of the tusks in the holotype skull, the facet itself does not appear to be quite vertical but seems to slope slightly backwards and downwards. A sloping wear could be produced only if there were a

TABLE 30. DIMENSIONS OF UPPER CANINES OF *NYANZACHOERUS PLICATUS*

Specimen No. (KP)	Maximum Diameter	Minimum Diameter
251 left	27.0	21.0
″ right	29.5	20.0
252 left	31.5	22.0
″ right	30.9	21.7
262	26.0	21.0
235 left	34.5	23.5

TABLE 31. DIMENSIONS OF LOWER INCISORS AND CANINES OF *NYANZACHOERUS PLICATUS* (Specimen KP 262)

		Length	Breadth
I_1	(root)	9.0	13.0
I_2	(root)	7.5	14.0
I_3	(root)	7.0	12.0
C_1	(in alveolus)		
	left	21.0	15.5
	right	22.0	15.5

strong propalinal component in the jaw action, of a type unknown elsewhere. It seems more likely that there has been some distortion in the holotype skull and that in fact the facet had the usual vertical orientation. The lower canines must therefore have flared outwards and upwards so that the tips were not quite vertical but sloped slightly outwards. Closed rooted canines have been recorded hitherto only in "*Promesochoerus mukiri*" Leakey (1965), but it is believed that *Nyanzachoerus pattersoni* also had upper canines with closed or nearly closed roots.

The Second Paratype

A number of closely associated fragments represent pieces of a skull and mandible of a very young adult (KNM–KP 262; Pl. 15). The fragments include a piece of left maxilla showing the canine with its characteristic shape. There is also a piece of the left parietal broken along the midline but including the upper rim of the orbit, the supra-orbital foramen, and part of the parietal crest behind the postorbital processes; it is thus possible to estimate the interorbital width as about 100 mm as compared with 116 mm for an estimate made on the older holotype skull. The upper rim of the orbit lies a trifle below the surface of the skull roof, which is almost flat, very much as in *Hylochoerus* and contrasting with the raised orbits of *Phacochoerus*. The parietal crest behind the orbit, however, runs sharply towards the axis of the skull, almost at 45°, very much as in *Phacochoerus*, and it would appear that the braincase was shortened in the same way as in the warthog. The parietal constriction must have been narrow.

There is a rather flattened mandibular symphysis containing the roots of the incisors, the root of the left canine, and the right canine lacking only the tip (Pl. 15A) (Table 31). The morphology of the symphysis matches that of the holotype mandible. The lower canines are unlike the usual sharp triangular lower canines of the suids and resemble the upper canines in general outline but are anteriorly a little tapered and posteriorly flattened or slightly grooved. Enamel is visible only on the upper surface and is weakly rugose and very thin. The canine, like the upper tusks, is more forwardly directed than those of either *Hylochoerus* or *Phacochoerus*. The roots are still open but might have closed later in life.

A portion of the right mandibular ramus contains the second molar, damaged anteriorly, and the third molar, damaged posteriorly but with the impression of the back of the tooth visible in the bone (Pl. 15D, E). Dimensions are given in Table 29. Both in size and in structure the third molar corresponds to that of the holotype. Each of the paired columns is divided into a lateral and an axial element separated by well-marked anterior and posterior grooves. The lateral element is bounded by the broadly curved outer wall of the pillar, which is fairly smooth and has thick enamel. The inner element has a rather crenulated or irregular axial wall. The anterior lingual pillar has its posterior axial corner nearly isolated by a deep vertical groove, almost giving the appearance of an extra median pillar (this feature is also apparent in specimen KP 254). The anterior buccal pillar has a smilar vertical groove, nearly isolating an anterior lobe that resembles an eccentric anterior pillar. The second molar is rather elongate, having a strong shelflike posterior cingulum that produces a trefoil-shaped enamel

TABLE 32. DIMENSIONS OF UPPER CHEEK TEETH OF *NYANZACHOERUS PLICATUS*

	Specimen No. (KP)		Stage of Wear	Length (L)	Breadth (B)	Height	L/B
P^2	257		Early	10.5	6.7	6.0	1.57
P^3							
	257	left	Moderate	22.5	18.0	14.0+	1.25
	"	right		22.5	18.2	14.5+	1.23
P^4							
	257	left	Moderate	18.4	19.8	14.0+	0.93
	"	right		18.2	20.3	14.5+	0.90
M^1							
	257	left	Very advanced	18.5	c19	3.0+	c0.98
	"	right		18.0	c19	2.5+	c0.95
M^2							
	262		Moderate	39.0	26.7	16.0+	1.46
	206		Moderate (Very weathered)	37.6	c27	12.0+	c1.4
	257	left	Advanced	32.1	25.5	7.0+	1.26
	"	right		32.8	26.2	7.5+	1.25
M^3							
	225	right	Early	68.0	c30	31.0	c2.25
	235	left	Moderate	63.5	31.5	25.0+	2.01
	257	left	Moderate	66.6	35.7	20.0+	1.86
	"	right		67.8	35.2	21.5+	1.92
	253		Moderately advanced	71.5	33.2	21.5+	2.15
Specimen KP 257							
	Length of premolar series			c46			
	Length of molar series			117			

island. The form of the pillars corresponds closely with those of the third molar.

An upper right second molar in early wear occludes perfectly with the lower teeth and provides a firm link between upper and lower tooth characters (Pl. 15 D, E). The lateral wall of the paired pillars is not as long as on the lower teeth, with the consequence that the axial element of the structure is longer than the lateral one. The lingual pillars have a decided and persistent stellate form, whereas the buccal pillars are more bell-shaped with an irregular axial wall. There is a strong posterior cingulum, like that in the lower second molar, and also a broad symmetrical anterior cingulum. The median pillar is irregular. Dimensions are given in Table 32.

The Third Paratype

This specimen comprises part of a skull, broken anteriorly immediately in front of the premolars, and posteriorly close to the supra-orbital foramina and through the back of the palate (KP 257; Pl. 13). The zygomatic arches are also lost. All the cheek teeth are preserved except for the right P^2.

The general morphology of the frontal and lacrimal areas corresponds well with the holotype. The muzzle is obviously narrow and has the same cross section as the holotype. At the same level of the zygoma the same sort of lateral "shoulders" are present. The beginning of the zygomatic arch lies high above the palatal plane, and the maxilla above M^2 is hollowed so that the lower edge of the arch is sharply defined. This resembles in some respects the condition in female warthogs. Below this rather high beginning of the flare, the zygoma descends to a low point above the middle of M^3, quite unlike any of the living African suids. The rest of the zygoma looks as if it were more hylochoerine than phacochoerine, and the basal portion expands laterally so much as to suggest that a zygomatic protuberance or knob must have been present, although too much is missing for this to be certain. The profile of the skull from the frontals towards the occiput must have resembled *Phacochoerus* to some extent, although the elevation of the cranium was not as exaggerated; the front of the snout did not droop in the warthog fashion and was relatively longer than in *Phacochoerus*. Some dimensions are given in Table 28 and a tentative restoration in Figure 7.

The elevation of the skull is reflected in the contours of the pterygoid and sphenoid areas above the back of the palate. The nasal passage is curiously narrowed above the third molar, possibly because the tooth is very wide and its roots restrict the space available. The palatine notch is not visible but must have been well behind the back of the third molar. The main foramina are level with the middle of M^3.

The upper dentition (Pl. 16) agrees excellently with the features seen in the M^2 of KP 262. The RP^3 is twisted into a position at right angles to its normal orientation, but the left one is in the normal position. The second premolar has also been twisted out of the normal orientation, but to a lesser degree. Measurements are given in Table 32.

P^2. The second premolar is a very small tooth. It is relatively broad with a central cone the full width of the crown; there are anterior and posterior ridges and possibly a secondary cone towards the back of the crown.

P^3. The third premolar has a stout main cusp with a moderately strong anterior cingulum on the anterolingual side. On the back of the tooth is a narrow high cingulum and there is a rounded postero-internal cusp.

P^4. This tooth is almost square and is built in the *Potamochoerus* fashion with a pair of buccal cones (paracone and metacone), apparently not widely separated and uniting into an island which, at least at this stage of wear, maintains a notch on the axial side. The lingual cone (protocone) is transversely narrower than the buccal cones, and produces an irregularly shaped enamel island similar to the buccal columns in the third molar, but laterally more compressed. There are moderate anterior and weak posterior cingula.

The M^1 are worn to dentine and no features can be distinguished.

M^2 is in advanced wear and the pattern is difficult to decipher, but there is nothing visible that conflicts with the details shown in the less worn tooth described in the second paratype.

M^3. The third molars are wide anteriorly and taper progressively towards the talon. There are three pairs of lateral pillars separated by single median pillars and there is a stout central talon pillar. Accessory columns rise from the base of the tooth between the second and third pairs of pillars on both sides and between the first and second pairs on the buccal side. The shape of the enamel islands is closely similar to that in the second molar KP 262 described above. A feature of the dentition which deserves comment is the rather marked upward taper from the base of the molars towards the crown; the occlusal width is thus 20 per cent narrower than the base in this specimen. The measurements are given in Table 32 and the teeth are illustrated in Plate 16.

Referred Specimens

A small assemblage of associated material, all numbered KP 235, very probably belonged to a single individual. There is an almost complete upper left third molar, in early wear, a piece of the right upper third molar, two parts of the mandible and pieces of both lower tusks, parts of the pelvis, a third cervical vertebra, and small fragments of skull and other bones.

The upper left third molar fits perfectly with the third molar of the mandible, so that there is no doubt about the identity. It matches closely in dimensions and structure the corresponding tooth in the skull KP 257. It has been sectioned half way down and the pattern is shown in Figure 9; photographs are given in Plate 17 and dimensions in Table 32. The other fragment represents the back half of the corresponding upper right molar.

The mandible has only two teeth reasonably well preserved. The left ramus is broken anteriorly and also behind the third molar, which is intact; the roots of P_2–M_2 are present. The right ramus is only a fragment, broken behind P_4, has the roots of P_3, the socket for a small P_2, and some of the socket for the canine. The third molar matches in structure the third molar in the second paratype, but the enamel is smoother and the convolutions in the axial region are less complex. It is illustrated in Plate 18 and the dimensions are given in Table 29. The P_4 in the right ramus fragment, undoubtedly of the same individual, lacks much of the lingual side. There is a fairly stout main cone, with a steep broad ridge extending to a rather pustulate anterior cingulum. There is a high posterior cingulum, bearing a stout cusp. A very large mandibular foramen is shown on the anterior part of the jaw fragment, lying below a point about 3 cm in front of the P_2 socket.

The canine fragments belong to a pair of lower tusks, the larger piece being 11 cm long and, as we judge by the slight curvature, is from the left side. Its cross section is subtriangular, with the upper and lower faces gently curved and the apex bluntly rounded; the posterior face is slightly hollowed (see Fig. 8). The maximum diameter near the base is 34.5 mm and the transverse dimension 23.5 mm.

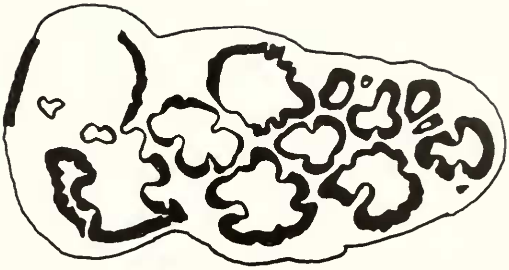

Figure 9. Enamel pattern on sectioned surface of isolated upper left third molar of *Nyanzachoerus plicatus* (see also Pl. 17). Nat. size.

Thin enamel is present on both the upper and the lower surfaces. In this respect it appears to differ from the juvenile tusks in the symphysis of KP 262, in which enamel is visible only on the upper surfaces, although it may well have been present on the lower surface in later life.

The two incomplete pelvic bones correspond in general morphology to those of *Hylochoerus* but are 20 per cent longer. The third cervical vertebra also agrees reasonably well with *Hylochoerus* in general form but is a good deal larger, perhaps by 15–20 per cent.

Four isolated upper molar teeth, or fragments, are also assigned to this species. One (KP 253) is a complete upper right third molar in moderate wear, corresponding very closely with the molars in skull KP 257, although a little larger (see Table 32; Pl. 17). Two upper third molars in early wear are numbered KP 225 and belong to a single individual. The RM^3, although damaged, is very similar to the upper molar KP 235, both in morphology and in dimensions (Table 32). Only the back half of the LM^3 is preserved. There is also a very rolled and weathered right upper second molar (KP 206) that can be assigned to the species as it corresponds to the same tooth in the skull KP 257.

An unworn right lower third molar (KP 254) lacks the front part of the first pair of pillars. When complete it was slightly larger than KP 262 but it displays the same structure. The talon shows a number of

TABLE 33. MEASUREMENTS ON POSSIBLE LOWER MILK DENTITION OF *NYANZACHOERUS PLICATUS* (KP 269)

	Length	Breadth	Height
Ldm$_3$	11.2	6.4	4.6+
Rdm$_3$	10.8	6.3	4.6+
Ldm$_4$	24.8	10.9	3.5+
Rdm$_4$	24.8	10.9	3.5+
RM$_1$	28.0 (23.0 at base)	16.8	14.5+

small accessory columns extending from one-third to one-half the height of the crown (Pl. 17).

The tip of a gently curved isolated canine (KP 203) has a flattened oval cross section and measures near the broken base 29.5 mm by 20.0 mm; the length from the damaged tip to the broken base is 10 cm. There is no enamel. On the inner side of the tip is a small wear facet. The curvature of the tooth matches that in the isolated canine referred to *N. plicatus* and the dimensions are similar. Although there are slight differences in the cross section, it seems probable that the tooth should be assigned to that species.

Possible Lower Milk Dentition

Two parts of the rami of a mandible (KP 269) possess on the left side dm$_3$ and dm$_4$ and on the right side dm$_{3-4}$ and M$_1$; there is also a fragment of LM$_1$; P$_3$ and P$_4$ are visible in the crypt on each side and they are not yet fully formed. Two fragments of an unerupted and incompletely formed M$_2$ were recovered and presumably came from the crypt. The form of the pillars and of the anterior cingulum in the M$_2$ makes it clear that the specimen does not belong to *N. pattersoni*. There is no known *N. plicatus* second molar in early wear available for comparison, but the structure of the anterior part of the M$_2$ is so like that of the unworn M$_3$ that it is reasonable to assign this milk dentition to *N. plicatus*.

The dm$_3$ differs from that of *N. pattersoni* in possessing a slightly stronger posterior cingulum on the lingual side, in being a little longer than the corresponding tooth in *N. pattersoni*, and in having wider lateral pillars. The M$_1$ is considerably longer than the M$_1$ of *N. pattersoni*, the extra length being in part due to elongation of the lateral pillars, in part to strong development of a posterior cingulum. The enamel figures are like those of adult teeth which have been assigned to *N. plicatus*, the lateral pillars being rather more folded than in *N. pattersoni*. Measurements are given in Table 33.

DISCUSSION

Although there can be no doubt that the material representing the species *plicatus* is very different from that assigned to *Nyanzachoerus pattersoni*, there is also the possibility that it belongs to a distinct genus. The third and fourth premolars are less enlarged than is the case in *N. pattersoni*, but they are nevertheless enlarged relative to *Sus* or *Potamochoerus*, as will be demonstrated later in this account. The lower canines are very similar to those of *N. pattersoni*. The material available is not sufficient to show whether there is any marked sexual dimorphism in *plicatus*, but the third paratype skull suggests that there was at least a fair degree of zygomatic inflation. The snout, though longer and thinner than that of *N. pattersoni*, shows the same general conformation, and the degree of elevation of the braincase is similar. The upper canines are oval in cross section, show no signs of enamel and have a very small pulp cavity; root formation clearly occurred early, possibly even earlier than in *N. pattersoni*. The teeth are constructed in a manner generally similar to those of *N. pattersoni*, and the main difference lies in the enlargement of the third molar and in the greater degree of complexity of the folding of the enamel in the molars, which provides the basis for the specific name. Although more complete material may make it possible to show that a different genus is represented, at the present time it seems reasonable to assign *plicatus* to the genus *Nyanzachoerus.*

It now transpires that a tooth of *N. plicatus* has been known for some time but could not be recognised. It is an upper right third molar from the Chiwondo Beds, near Lake Nyasa, Malawi, and it was described by Hopwood in 1931 as the lower third molar of a large *Hylochoerus* (BMNH M 14121). Leakey (1958) considered that it was probably an upper third molar of *Mesochoerus paiceae* (the upper dentition of which is not certainly known). The specimen has all the features found in the third paratype but is a little more robust, and the talon is broader and somewhat more complex. It is cracked and weathered and there seems to have been some slight expansion of the crown as a result of wedging by mineral growth, so that the original dimensions may have been a millimetre or two less than the present length of 73.5 mm and maximum anterior breadth of 37.0 mm. The tooth is moderately well worn and the present maximum height, at the talon, is 21 mm, but it is clear that the intact crown was only about 30 mm high. The same upward taper is seen as in the Kanapoi material and the specific identity is not in doubt.

THE NEW *NYANZACHOERUS* FROM LOTHAGAM

Nyanzachoerus tulotos sp. nov.*

Text-figure 10; Plates 19–25

Diagnosis. A species of *Nyanzachoerus* about the size of the extant *Hylochoerus*, but more robust. Both upper and lower first premolars present; third and fourth premolars large, P^4 approximately as broad as M^3. Third molars relatively low-crowned and composed of only two pairs of lateral cusps, together with a small talon or talonid. In both upper and lower jaws, the premolar series P2–P4 is over 70 per cent of the length of the molar series; P_4 is more than half as long as M_3. Diastema from lower canine to P_2 about three quarters the length of the premolar series P_2–P_4. In the male the preorbital ridges are strongly marked; the maxillary flanges around the canines, and the nasopremaxillary thickenings, are large, the former rising to the level of the dorsal surface of the snout. Skull table broad but lightly built, in striking contrast to the heavy muzzle region. Zygomatic protuberances of moderate size and, while considerably expanded laterally, not deep dorsoventrally; viewed from the side they are not significantly deeper near the posterior than near the anterior end, and the lower margin is approximately horizontal.

Holotype. KNM–LT 316; an almost complete skull, regarded as male.

Paratype. KNM–LT 302; incomplete left and right mandibular rami, regarded as male. KNM–LT 287: damaged mandible, including symphysis and lower canines, regarded as male. KNM–LT 295: mandible of adult with symphysis damaged but showing very small lower canines, together with a loose incisor, regarded as female.

Locality. Lothagam, northwestern Kenya.

Horizon. Lower part of deltaic series (Unit 1, Member B), Lothagam sediments; probably Middle to Upper Pliocene.

Remarks. As was indicated in the introduction, and shown diagrammatically in Figure 2, the fossil suid material has come from two zones in the deltaic series of Unit 1. The most complete specimens, and the best range of material, came from Member B, below the red marker and tuff marker; these are regarded as the "typical" *Nyanzachoerus tulotos*, and the account that follows is based on this material only. The specimens from Member C show some differences and they will be discussed separately and the measurements will be shown separately in the relevant tables.

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* *N. tulotos* has been referred to in several preliminary faunal lists as *Nyanzachoerus* species "C."

REFERRED SPECIMENS FROM UNIT 1, MEMBER B

KNM–LT 282: isolated, unerupted LM_3. LT 283: isolated, damaged M_3. LT 288: much crushed mandibular symphysis and right ramus, including canines and roots of two incisors, damaged remains of premolars and heavily damaged molars. LT 290: several isolated teeth, not belonging to the same individual, comprising LP_4, tip of right lower canine, two damaged RM^3, and a fragment of maxilla with RP^3 and RP^4. LT 291: right mandibular ramus with stump of canine, RP_2–M_1 and the stump of RM_2. LT 300: right mandibular ramus with RP_3–M_2 and the anterior part of M_3; the two premolars are badly damaged. LT 301: damaged fragments, including LP_3, LP_4, RP_4, remains of LM_3 and RM_3, a fragment of lower canine. LT 303: left mandibular ramus with LP_4, LM_3 and roots of LM_1 and LM_2. LT 305: damaged right mandibular ramus with base of canine, roots of RP_2 and RP_3, and anterior part of RM_3. LT 319: isolated unerupted M^3. LT 321: isolated RM^3.

DESCRIPTION

The Holotype Skull

Specimen KNM–LT 316 consists of a skull, somewhat cracked and crushed dorsoventrally but almost complete. The only parts missing are the greater part of the occiput, together with the posterior regions of the skull table and left zygoma, and the tips of the nasals. The incisors, canines, and RP^1 are missing but all the other cheek teeth are present.

The skull belongs to a young adult, with the third molars fully erupted but not much worn. It is of moderate size, with an estimated vertex length of 425 mm, which is about the size of a large *Hylochoerus* skull, although the fossil is wider and more robust (Table 34). The presence of very large maxillary flanges whose dorsal wings extend almost as high as the snout, together with corresponding thickenings on the muzzle at the nasopremaxillary suture, is at once reminiscent of the condition in a male bushpig. It is because of these features that the skull is regarded as belonging to a male. There are, however, differences in detail from the condition in the bushpig; the dorsal wings of the very elongated maxillary flanges are situated almost directly above the canine alveoli, instead of somewhat behind the tusks, and they rise almost vertically without a significant backward rake. The flanges more closely resemble a hypertrophied version of the relatively small ones that occur in *Hylochoerus* than they do those of the bushpig and are, indeed, very like those of *Sus strozzi*. Another resemblance to *Hylochoerus* is the distinct bulge on the premaxilla in front of the flanges, which lies between the tendons of the levator rostri and dilator naris lateralis muscles. In the bushpig, with its very small rhinarium, these tendons lie closer together and the vertical surface of the premaxilla is almost flat.

Behind the maxillary flanges, the muzzle shows only a slight constriction at the level of the pre-orbital foramina. Although there has been some crushing and distortion in this region, it is clear that the upper surface of the muzzle was slightly convex and that rounded "shoulders" separated this from the more vertical side walls. As they pass backwards, the shoulders become more distinct and are continuous with pre-orbital ridges of the same sort as occur in *Nyanzachoerus pattersoni*, but they are much larger in the Lothagam species.

The whole posterior region of the skull is extremely broad. The width across the zygomata is three-quarters of the basilar length, and the maximal width across the frontals is almost 40 per cent of the total length of the skull. The supra-orbital foramina lie just anterior to the orbits; at this level the enlarged pre-orbital ridges

TABLE 34. MEASUREMENTS ON HOLOTYPE SKULL OF *NYANZACHOERUS TULOTOS* COMPARED WITH *HYLOCHOERUS MEINERTZHAGENI*

	Holotype	*Hylochoerus*
	LT 316	MA 1 H 1
Vertex length	425e	428
Basilar length	402	375
Bizygomatic breadth	295	246
Greatest breadth across nasals	63	56.5
Breadth of muzzle between infraorbital foramina	50	71
Parietal constriction	88e	96
Breadth across postorbital processes	166	125
Height of top of orbit above palatal plane left	92	
		115
right	103	
Palatal length	316	283
Breadth of palate		
between M^3–M^3	36	46
between P^2–P^2	38	59
Palatine notch position*	46	83
Palatine notch width	23	40.5
Precanine breadth across premaxillae	90	74
Breadth between back of I^3–I^3	77	51.5
Diastema C–P^1	11	–
C–P^2	39	35
Length of premolar series P^1–P^4	93	–
P^2–P^4	63.5	24.5
Length of molar series	90	77

* Distance from anterior back of palatine notch to line joining boundary between M^2 and M^3

terminate and the surface of the skull, from the orbits back, is smooth and gently concave, very much as in *Phacochoerus*. The orbits, however, are not raised above the level of the skull table, but, as in *Hylochoerus*, lie slightly lower than the parietal crest. The latter slopes gently upwards and it is clear that, as in *Hylochoerus*, the parietal crest was the highest point of the skull.

The zygomata originate on the muzzle at the level of P^4 and from this point flare outwards sharply, very much like an exaggerated version of *Hylochoerus*. Below and just behind the orbit, the jugal is expanded laterally and thickened dorsoventrally to form a zygomatic protuberance that, although smaller than that of *Nyanzachoerus pattersoni*, is both larger and more posteriorly situated than the zygomatic thickening on *Hylochoerus*. The surface of the bone is not very well preserved, but it certainly cannot have been as rugose as in the zygoma of *Hylochoerus*. It therefore seems improbable that any extensive zygomatic wart was present, although there may have been some thickening of the skin overlying the protuberance.

Although the occiput is damaged, sufficient of the temporalis attachment is present to show that this muscle must have been of approximately hylochoerine proportions. The shape of the orbits has been much distorted by crushing but one distinctive feature is preserved, to wit, that in front of the postorbital process the upper margin is dilated and projects slightly to overhang the actual eye socket. This must have given the eyes, in life, an unusually deep-set appearance.

The curiously "lumpy" appearance of the skull, and also of the teeth, forms the basis for the specific name, derived from the Greek (τυλωτός) meaning a knob, lump, or callous.

The character of the canine alveoli, small with large maxillary flanges, together with the unreduced upper incisors, gives the anterior part of the palate a somewhat potamochoeroid aspect. The snout, however, is much less specialized as a digging organ than in the bushpig and tapers gently from the margin of the canine alveolus to the anterior end, instead of being narrow and parallel sided. There is very little widening of the palate at the level of the canines, and the blood vessel grooves therefore run an almost parallel course from the anterior to the posterior palatal foramina. The palatine notch is very similar to that of *Potamochoerus*: it does not lie far behind the third molars and the posterior edge of the palatines bends upwards sharply beneath the nasal passage. The bullae resemble those of *N. pattersoni*, being laterally compressed and ending anteroventrally in a sharp point, but they are relatively larger. The glenoids are only slightly raised above the palatal plane and are wide from front to back—both of which facts indicate that the jaw movement was not a specialised sideways grinding action. The lower surface of the zygoma is flat and extremely broad, but the surface preservation is not good enough to permit the limits of the masseter origin to be made out.

Although none of the incisors is preserved, the alveoli show that three pairs were present and that they were unequal in size. Both *Hylochoerus* and *Phacochoerus* retain only one pair of permanent upper incisors. The canines, too, are represented only by alveoli, but these show that the tusks must have been small and much flattened dorsoventrally, and they probably rooted early. Details of the tooth structures are given later in the section on the upper dentition.

The First Paratype Mandible

Specimen KNM–LT 302 comprises portions of right and left mandibular rami. The right ramus includes P_3–M_3 and the left one has P_2–M_1, together with some remnants of the canine. The relatively large size of the tusk suggests that the jaw belonged to a male, and in both size and morphological characteristics the specimen agrees very well with the type skull.

The corpus of the mandible is rather heavy, its thickness at the level of P_4/M_1 being about 42 mm. Just sufficient of the right ramus is preserved to show that behind M_3 the inner margin of the bone curves abruptly outwards; this is to be expected if the bone forming the angle was light, as in *N. pattersoni*. Nothing of the symphysis is preserved and the portion of the root of the canine that remains is much damaged. The latter, however, is sufficient to show that the maximal diameter of the tusk within the aveolus cannot have been less than 20 mm and was probably rather more. The dimensions of the teeth are included in the appropriate tables and the jaw is illustrated in Plates 20 and 22.

The Second Paratype Mandible

Specimen KNM–LT 287 is a somewhat damaged mandible, including the symphysis and lower canines, and is considered to belong to a male. The jaw is rather crushed, the anterior margin is eroded, and of the incisors only some fragments of the central pair remain. On the right, the ramus is preserved to a level a little behind the third molar, but of the cheek teeth only P_1–P_3 and a damaged P_4 remain; the molars have been broken away and only traces of the roots exist. On the left, the ramus extends only to the level of P_4; P_1 has been broken off at the alveolar margin; P_2 is present, together with the much cracked P_3 (Pl. 20).

The preserved second and third premolars agree very closely with those of the first paratype; the length of the cheek tooth series and the thickness of the jaw are similar. There can be little doubt that the two belong to the same species, and the size of the canines in the present specimen suggests that it too is a male. Although the cheek teeth are much damaged, this specimen complements the first paratype and provides information about the characters of the symphysial region, missing in the latter.

A little more of the posterior part of the jaw is present in this specimen than in the first paratype and this shows that, as indicated in the latter, the thick corpus narrows very rapidly behind the tooth row, where the masseter and pterygoideus muscles are inserted. The preserved part of the lower margin of the angle, although ridged in relation to these muscle insertions, is very slender, exactly as in the jaws of the species of *Nyanzachoerus* from Kanapoi.

The symphysis is elongated. It extends back to the level of the anterior root of P_3 and its length, measured along the curved ventral surface, is approximately 150 mm.

The general shape is roughly similar to that of the bushpig but the constriction behind the canines is less marked and the anterior end of the jaw is more pointed, so that between the canines the bone forms a pointed extension and the incisors do not lie virtually in a straight line, as they do in the bushpig. This accords well with the tapering snout region in the type skull. The anterior mental foramina lie behind the level of the posterior end of the canine alveoli, and, in front of them, the bone extends for at least 40 mm. This is in contrast to the bushpig, where the central region is truncated, the incisors lie almost in line, and the distance between the anterior mental foramina and the alveoli of the central incisors is consequently very short. The insertion of the protractor muscle of the lower lip in the fossil is extremely like that of the bushpig, and, at the posterior margin of the symphysis, the insertions of the geniohyoideus and genioglossus are clearly marked. They are deeply inset just above the lower border of the posterior wall of the symphysis exactly as they are in the bushpig. The dorsal aspect of the symphysis is also distinctly potamochoeroid, with the same differences as noted above, the constriction behind the canines being a little less marked and the margin in front of the canines more pointed.

The Third Paratype Jaw

Specimen KNM–LT 295 is the mandible of an adult with very small canines, regarded consequently as belonging to a female; associated with it is an isolated left central incisor. The jaw is broken off on either side a little behind the third molars and the anterior part of the symphysis is missing, but it is otherwise complete (Pl. 20). The incisors are missing, except for the root of the right I_1, and the canines, first premolars, and left second premolar are broken off at the alveolar margin. The other cheek teeth are present on both sides (Pl. 23) and their measurements are included in the relevant tables.

A very peculiar feature of the mandible (KNM–LT 295) is the asymmetry of the jaw. On the left side the rising curve of the ascending ramus is approximately 9 cm behind the back of the third molar. On the right side the corresponding point is only 3.5 cm behind the third molar, so that the whole jaw is shortened on this side, although the third molars are equidistant from the symphysis. There is no possibility that this is the result of post-mortem distortion, as is attested by the normality of the muscle impressions. It is thus clear that the ascending ramus was much foreshortened. It would be expected that such malformation would have effects on the jaw movement, and hence on the teeth. Contrary to this expectation, the teeth are worn in a completely normal manner, indicating either that the mandibular condyle was nevertheless in a normal position (which is difficult to imagine), or that there were compensating distortions in the skull.

This specimen differs from the second paratype jaw mainly in the small size of the canine, the maximal diameter being 14.8 mm as compared with 22.5 mm in the latter. It is this feature that is taken to indicate that specimen LT 295 should be identified as belonging to a female. The fact that the cheek teeth in this specimen are, in general, rather small should not be regarded as characteristic of females. As may be seen from Table 40, there are other specimens in which the canines are very small, but the dimensions of the cheek teeth are not below the mean values.

Specimen LT 295 shows the usual heavy, thickened rami, thinning away sharply behind the third molars. Presumably in relation to the small canines, the whole symphysial region, although of the same general form as that of the second paratype, is much shorter. Although the anterior margin is missing, the presence of one central incisor showing the enamel line makes it possible to estimate the length of the symphysis with considerable confi-

TABLE 35. *NYANZACHOERUS TULOTOS* DIMENSIONS OF UPPER INCISORS

Specimen No. (LT)	Tooth	Transverse (length)	Anteroposterior (breadth)	Height
295	RI^1	21.5	10.8	16.0+
326	RI^1	21.3	10.5	12.8+
316	LI^1 alveolus	18.8	15.0	–
	RI^1 alveolus	18.2	14.6	–
	LI^2 alveolus	20.8	11.4	–
	RI^2 alveolus	20.2	11.5	–
	LI^3 alveolus	19.4	c10.6	–
	RI^3 alveolus	18.6	12.6	–

dence. It must have measured approximately 105 mm, as compared with 150 mm in the second paratype. The anterior mental foramina lie further forward than in the male jaw, being situated approximately at the level of the anterior margin of the canine alveolus, instead of slightly behind the posterior margin. The origins of the geniohyoid and genioglossus muscles, as in the male, are strongly marked and deeply inset, like those of the bushpig.

The Upper Dentition

Only a single upper incisor tooth, belonging to specimen LT 295, is known from the lower deltaic beds. This is a left central incisor; its general form is very much like that of the bushpig, but on the mesial two-thirds of the lingual face there is a low cingulum. An almost identical right upper incisor tooth (LT 326) occurs in the upper deltaic beds. Alveoli are present in the holotype and their measurements, together with those of the two actual teeth, are given in Table 35.

No upper canines are known but the dimensions of the alveoli of the type skull (given in Table 36) indicate that they cannot have been very large. The flattened oval shape has already been mentioned. A canine found with the holotype is almost round in cross section and does not fit the skull.

TABLE 36. *NYANZACHOERUS TULOTOS* DIMENSIONS OF UPPER CANINES

Specimen No. (LT)	Position	Maximum	Minimum
316	Left alveolus	41.5	29.0
	Right alveolus	40.7	34.0

P^1 and P^2 are known only from the type skull. P^1 is present only on the left side. It is a small elongated tooth with an ill-defined main cusp and a posterolingual cingulum. It lies midway between the canine and the second premolar, separated from each by a short diastema. On the right, an alveolus is present in the corresponding position.

P^2 is a small, elongated tooth, composed of a rather low main cusp surrounded by a cingulum to which it is linked by rather poorly defined anterior and posterior crests. At the posterior end, the cingulum extends lingually and a small fovea intervenes between it and the main cusp: the outline of the tooth is thus subtriangular. Although there is considerable wear on the more posterior teeth of the type skull, P^1 and P^2 are almost unworn and they cannot have been of much functional value.

P^3 is a large tooth, almost as broad as it is long (Table 37). In the type specimen the large main cusp is almost circular in cross section and is surrounded by a much crenulated cingulum. The cingulum is broadest at the antero- and posterolingual margins and thins away on the outer surface over the large buccal root. In the referred specimen (LT 290) the cingulum is not quite so well developed; it is absent

TABLE 37. *NYANZACHOERUS TULOTOS* DIMENSIONS OF UPPER PREMOLARS

FROM MEMBER B

	Specimen No. (LT)		Stage of Wear	Length	Breadth	Height
P^1						
	316	left	Slight	12.1	6.4	5.9
	"	right	Alveolus	16.5	7.8	–
P^2						
	316	left	Slight	15.2	10.5	c8
	"	right		15.4	10.8	c8
P^3						
	290		Moderate	24.8	22.0	14.5+
	316	left	Moderately heavy	24.5	23.7	c16 +
	"	right		24.5	23.0	c17 +
P^4						
	290		Moderate	20.6	25.0	13.2+
	316	left	Moderately heavy	19.8	28.5	14.3+
	"	right		19.9	26.4	14.6+

FROM MEMBER C

	Specimen No. (LT)	Stage of Wear	Length	Breadth	Height
P^3					
	310	Early	29.4	29.3	20.6
	313	Moderate	31.0	31e	17.5e+
P^4					
	310	Moderate	22.7	28.0	15.0+
	313	Moderately heavy	22.5	30.8	10.6+

on the whole of the buccal surface and thins away in the centre of the lingual surface.

P^4 is also large. The main cusp is transversely elongated and the tooth is broader than it is long. Anteriorly and posteriorly a crenulated cingulum embraces the main cusp but thins away on the buccal and lingual faces, so that the main cusp accounts for the whole width of the base of the tooth. In the referred specimen, LT 290, the cingulum is smaller. Towards the apex the main cusp divides into the separate lingual and buccal elements typical of nyanzachoerine fourth premolars. In the more heavily worn type specimen these have fused to give a single wear facet, which on the buccal side is a smooth semicircle but lingually is irregularly folded where it contacts the cingulum. Dimensions of premolars are given in Table 37.

The first and second molars are known only from the type specimen (Table 38). M^1 is heavily worn but clearly consisted of the usual anterior and posterior pairs of cusps. A small median element may well have been present but the tooth is so heavily worn that it is no longer distinct.

M^2 is a large tooth with a crown composed of anterior and posterior pairs of cusps and anterior and posterior cingular complexes. A small median cusp has almost fused with the posterior cusps. The outlines of the wear facets on the main cusps are roughly circular with some slight irregularities towards the centre of the tooth, where they contact the median element.

TABLE 38. *NYANZACHOERUS TULOTOS* DIMENSIONS OF UPPER FIRST AND SECOND MOLARS

FROM MEMBER B

Specimen No. (LT)		Stage of Wear	Length	Breadth	Height
M^1					
316	left	Heavy	23.0	22.0	9.3+
"	right		21.8	21.3	8.0+
M^2					
316	left	Moderate	28.6	28.9	11.5+
"	right		28.7	27.2	11.9+

FROM MEMBER C

Specimen No. (LT)	Stage of Wear	Length	Breadth	Height
M^1				
310	Moderate	23.3	21.6	6.5+
313	Very heavy	26.3	24.5	6.3+
M^2				
293	Moderate	31.3e	27.2	12.5+
313	Moderate	35.6	31.8	7.5+

M^3 is a rather low-crowned tooth, very similar in structure to that of *Potamochoerus*. Two main pairs of cusps are separated by a lower, rather ill-defined median cusp. Anteriorly there is a cingular complex and posteriorly the talon is formed by a single terminal cusp, together with a few ill-defined auxiliary cusplets on the posterobuccal face. In none of the specimens is the wear on the cusps very heavy, but in the type and in the damaged specimen, LT 283, it is enough to expose the form of the pillars. These are stout and very like those of *Potamochoerus* with an infolded rosette form, but the folding is more strongly marked than in the bushpig, especially on the lingual cusps. Dimensions are given in Table 39.

The Lower Dentition

The lower incisors are represented by only a few root stumps and alveoli in the

TABLE 39. *NYANZACHOERUS TULOTOS* DIMENSIONS OF UPPER THIRD MOLARS

FROM MEMBER B

Specimen No. (LT)		Stage of wear	Length	Breadth		Height	
				Anterior	Talon	Anterior	Maximum
319		Unworn	45.0	31.5e	15.2	19.0e	19.0
321		Early	43.0	28.6	14.8	18.0+	18.0+
290B		Early	40.0e	29.0	14.6	16.0+	18.5
290A		Moderate	41.0e	26.7	15.8	11.5+	11.5
316	left	Moderate	41.5e	27.0	22.8	16.1+	16.1+
"	right	Moderate	38.0	27.4	23.2	16.0+	16.0+
283		Heavy	39.4	c27	21.6	–	–
Mean			41.2	28.6	14.8		
S.D.			2.172	1.637			

FROM MEMBER C

Specimen No. (LT)	Stage of Wear	Length	Breadth		Height	
			Anterior	Talon	Anterior	Maximum
326	Unerupted	45.5e	31.5e	–	19.5	19.5
286	Early	46.1	32.0	17.1	16.6+	21.1
324	Moderately early	42.3	29.5	15.5	19.5+	19.5+
313	Moderate	48.8	33.7	19.5	15.0+	17.3+
293	Moderate	44.3	30.5	15.0	16.8+	18.2+
307	Moderately heavy	45.6	31.5	15.7	13.3+	14.0+
Mean		45.4	31.5	16.6		
S.D.		1.961	1.295			

TABLE 40. *NYANZACHOERUS TULOTOS* DIMENSIONS OF LOWER CANINES

Specimen No. (LT)	Position	Maximum	Minimum	Length
291	right alveolus	17.2	11.0	–
305	right	22.0	c17.5	?
295	right	c16.5	c14.0	?
290A	left	21.3	15.0	74+
287	left	23.2	21.5	c80
"	right	22.5	20.5	c78
288	left	24.0	22.0	c85
"	right	25.5	22.0	c91

second and third paratypes and in specimen LT 288. These indicate that I_1 and I_2 were large and I_3 a little smaller. As already mentioned, the front of the symphysis is somewhat pointed and the incisors do not lie in a straight line.

Canines are present in the second paratype and in specimens LT 288 and 305; LT 290 includes an isolated canine tip. Roots are preserved in the third paratype (LT 295) and in specimens LT 300 and 291. As can be seen from the measurements given in Table 40, the roots in the third paratype and in specimen LT 291 are considerably smaller than in the other specimens. As already noted, this is interpreted as sexual dimorphism, and the two specimens with the small canines are regarded as female. The small tusks are known only from the broken off stumps included in these two specimens, but complete examples of the larger, presumed male, tusks are preserved. As can be seen from Table 40, even these are relatively small, the largest of them (specimen LT 288) measuring only 91 mm from alveolus to tip along the curved outer margin and having a maximum diameter of 25.5 mm. The tusks are more rounded than those of the bushpig; both upper and lower faces are gently convex, and where the two meet anteriorly, they do so smoothly without any sharp crest. Both are covered with enamel that bears fine cross striations, but no enamel is present on the posterior face (Fig. 10). The tusks emerge from the jaw at much the same angle as those of *Potamochoerus* and the wear facets of the two also show some similarity. In *Phacochoerus* the wear facet is a single almost flat vertical surface that looks as though it were made by a single clean cut. In *Potamochoerus* the distal part of the facet is similar but proximally it curves outwards rather irregularly, as though hacked out by a number of individual cuts. This difference, of course, reflects the specialized sideways grinding of *Phacochoerus* and the more rotatory action of the *Potamochoerus* jaw. It is the back-and-forth component of the movement that is responsible for the basal excavation in the wear facet of the latter. In the fossil, the potamochoeroid basal excavation is present, but is distinctly less marked than in the extant bushpig. This is

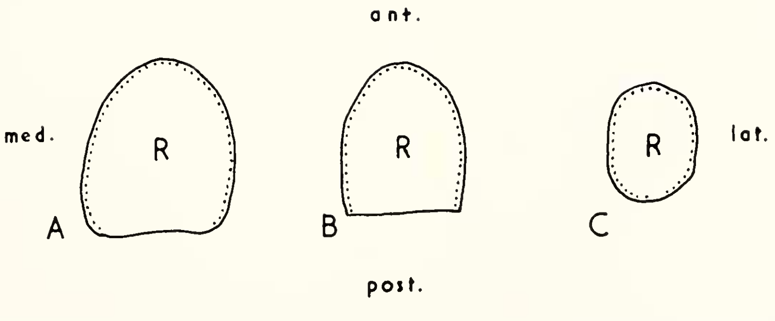


Figure 10. Sections of right lower canines of *Nyanzachoerus tulotos*. A is from the 2nd paratype (presumed male) and shows the shape at the alveolar border; B is the same tooth, 2 cm higher up, and shows the flat posterior wear facet. C is from the 3rd paratype (presumed female) and, although taken at the alveolar border, is close to the tip of the tooth and does not represent the final adult shape. Nat. size. Abbreviations as in Fig. 5.

Table 41. *Nyanzachoerus tulotos* dimensions of lower P_1

Specimen No. (LT)		Position	Length	Breadth	Height
291		root alveolus	c11.0	–	–
295	right	root alveolus	10.5	6.5	–
290A	left	broken	c11.0	c6.5	–
	right	moderate	10.1	6.0	5.5+

Table 42. *Nyanzachoerus tulotos* dimensions of lower P_2

Specimen No. (LT)		Stage of wear	Length	Breadth	Height
291		Slight	14.3	8.1	8.2
302	left	Slight	15.5	8.2	6.0+
295	left	Root	(14.5)	–	–
	right	Slight	15.0	7.6	6.0
287	left	Slight	15.3	8.8	7.0
	right		15.0	7.8	7.0
288	right	Root	(e14e)	(e8)	–
Mean			15.0	8.1	
S.D.			0.407	0.409	

in agreement with the characters of the glenoid in the type skull, which also suggests relatively unspecialized jaw action.

P_1 is present only in specimen LT 287 but broken off root stumps in other specimens show that it was regularly present. It lies midway between the canines and P_2 and is approximately oval, with a low main cusp and an anterior crest. Measurements are given in Table 41.

P_2 is a small elongated tooth with a low central cusp, joined by anterior and posterior ridges to low cingula, the posterior one of which bears a low cingular cusp (Table 42).

P_3 is large, with a somewhat backwardly raked conical main cusp. Anteriorly this is linked by a crest to an anterior cingulum that rises to a small pointed cusp where it meets the crest. Posteriorly, there is a broader, higher cingulum, the apex of which forms a small posterior cusp. In the almost unworn specimen LT 291 this rises to about half the height of the main cusp. Early wear on this tooth produces a backwardly sloping facet. As a result the posterior cingular cusp soon becomes abraded and its wear facet unites with that of the main cusp. Dimensions appear in Table 43.

P_4 is a broad, roughly rectangular tooth, composed of a strong main cusp, with slightly crenulated anterior and posterior cingula. The posterior cingulum bears a small cusp rising to at least three-quarters of the height of the main cusp. Measurements are given in Table 44.

M_1 is relatively small (Table 45). It has the usual anterior and posterior pairs of

Table 43. *Nyanzachoerus tulotos* dimensions of lower P_3

Specimen No. (LT)		Stage of wear	Length	Breadth	Height
291		Slight	28.0	22.0	27.0
305		Root	(30.5e)	(25e)	–
302	left	Moderate	29.0	23.3	25.0
"	right		29.2	23.6	25.0+
295	left	Moderate	26.0	19.1	20.7+
"	right		24.2	17.8	19.7
287	left	Moderately heavy	c30.0	c22.0	24.5+
"	right		28.0	21.8	24.5
300		Moderately heavy	25.0	18.8e	16.0+
301		Heavy	24.3	20.4	19.0+
288	right	Heavy	c29.5	20.5+	10.0+
Mean			27.3	20.9	
S.D.			2.126	1.944	

Table 44. *Nyanzachoerus tulotos* dimensions of lower P_4

Specimen No. (LT)	Stage of wear	Length	Breadth	Height
291	Slight	22.3	22.3	25.2+
305	Moderate	25.6	22.2	21.8+
302 left	Moderate	25.6	23.3	17.5+
" right		25.2	23.2	16.4+
295 left	Moderate	22.0	20.0	16.0+
		23.4	19.4	15.6+
303 right	Moderate	22.7	21.4	19.5+
290A	Moderate	22.3	19.8	16.6+
287 right	Moderately heavy	c28.0	24.0	21.5+
300	Moderately heavy	24.6	19.7c	15.3+
301	Heavy	23.7	21.6	9.8+
288	Heavy	c23.8	(20.5+)	8.5+
Mean		24.1	21.5	
S.D.		1.701	1.551	

cusps, and in the less worn specimens a posterior cingulum and traces of a very small anterior one are visible. A small median element becomes united with the posterior cusps before wear has proceeded very far.

M_2 has the usual structure of a pair of anterior and a pair of posterior cusps, separated by a smaller median element. Anteriorly there is only a very weak, slightly crenulated cingulum and posteriorly a much larger cingular complex, with a large cingular cusp. The cusps wear to an irregular rosette pattern with the outer margin smooth and the axial margin slightly indented. Measurements are given in Table 46.

M_3 is low crowned. The body of the tooth is composed of two pairs of lateral cusps, separated by a small median. Behind these lies a talonid consisting of a median and a pair of small posterior cusps, together with one or more very small cusplets. There is a crenulated anterior cingular complex and in the spaces in front of and behind the second buccal cusps are a few small, irregular cusplets. An unerupted tooth (LT 282) has a crown height of 21.2 mm, which is just a little less than the anterior breadth (Table 47).

Table 45. *Nyanzachoerus tulotos* dimensions of lower M_1

Specimen No. (LT)	Stage of wear	Length	Breadth	Height
291	Moderately early	21.1	17.2	11.1+
305	Moderate	22.1	17.3	9.5c+
302 left	Moderate	20.9	17.6	9.3+
" right		21.6	17.4	8.2+
295 left	Advanced	20.0	15.3	7.8+
" right		19.1	15.6	7.0+
300	Advanced	18.1	15.4	7.5+
288	Extreme	18.5	(c16.0)	–
Mean		20.2	16.5	
S.D.		1.388	0.985	

TABLE 46. *NYANZACHOERUS TULOTOS* DIMENSIONS OF LOWER M_2

FROM MEMBER B

Specimen No. (LT)	Stage of wear	Length	Breadth	Height
291	Moderately early	–	22.5	15.7+
305	Moderately early	30.7	21.0	15.5+
302	Moderate	28.3	22.0	15.5+
295 left	Moderate	27.5	21.2	11.8+
" right		27.0	20.3	11.7+
300	Advanced	26.0	22.3	9.3+
288	Extreme	23.0	c22.0	–
Mean		27.1	21.6	
S.D.		2.334	0.748	

FROM MEMBER C

Specimen No. (LT)	Stage of wear	Length	Breadth	Height
309	Roots	(30e)		
296	Early	26.7	20.3	15.5

Possible Referred Material

There are also a few other specimens in the collection from Member B that probably belong to *N. tulotos* but have not been included in the above account.

Specimen LT 306 consists of scraps of a skull and pieces of mandible. Recognisable are a left P^3 and P^4 in advanced wear and matching teeth of the right side, a well-worn LM^3 and a fragment of well-

TABLE 47. *NYANZACHOERUS TULOTOS* DIMENSIONS OF LOWER M_3

FROM MEMBER B

Specimen No. (LT)	Stage of wear	Length	Breadth		Height	
			Anterior	Talon	Anterior	Maximum
282	Unerupted	39.0	22.5	14.8	21.2	21.2
305	Moderately early	45.5e	24.3	–	19.0+	19.0+
302 right	Moderate	43.6	22.2	16.6	18.5+	18.5+
295 left	Moderate	41.0	23.5	18.7	17.0+	17.0+
right		41.1	23.5	17.4	16.3+	16.3+
303	Moderate	36.7	22.5	13.7	13.0+	13.0+
287	Roots only	(47e)	–	–	–	–
300	Moderately advanced	43.0e	24.4	–	10.8+	–
288	Extreme	42.8	22.7	15.5	6.5+	7.0+
301	Extreme	c43.0	c24.5	c14.8	–	8.0+
Mean		41.7	23.3	15.9		
S.D.		2.496	0.866			

FROM MEMBER C

Specimen No. (LT)	Stage of wear	Length	Breadth		Height	
			Anterior	Talon	Anterior	Maximum
309	Moderate	48.8	24.0	19.5	19.0+	19.0+

TABLE 48. AVERAGE DIMENSIONS OF UPPER CHEEK TEETH OF *NYANZACHOERUS TULOTOS*

		FROM MEMBER B			FROM MEMBER C		
		Range		Mean	Range		Mean
P^1	length (L)	12.1	(1)*	12.1			
	breadth (B)	6.4		6.4			
	L/B	1.90		1.90			
P^2	length	15.2 –15.4	(2)	15.3			
	breadth	10.5 –10.8		10.7			
	L/B	1.42– 1.45		1.44			
P^3	length	24.5 –24.8	(3)	24.6	29.4 – 31.0	(2)	30.2
	breadth	22.0 –23.7		22.9	29.3 – 31.0		30.2
	L/B	1.03– 1.12		1.07	1.00		1.00
P^4	length	19.8 –20.6	(3)	20.1	22.5 – 22.7	(2)	22.6
	breadth	25.0 –28.5		26.6	28.0 – 30.8		29.4
	L/B	0.70– 0.83		0.76	0.73– 0.81		0.77
M^1	length	21.8 –23.0	(2)	22.4	23.3 – 26.3	(2)	24.8
	breadth	21.3 –22.0		21.7	21.6 – 24.5		23.1
	L/B	1.01– 1.04		1.03	1.07– 1.08		1.08
M^2	length	28.6 –27.8	(2)	28.7	31.3 – 35.6	(2)	33.5
	breadth	27.2 –28.9		28.1	27.2 – 31.8		29.5
	L/B	0.99– 1.05		1.03	1.12– 1.15		1.14
M^3	length	38.0 –45.0	(8)**	41.2	42.3 – 48.8	(6)**	45.4
	breadth	26.7 –31.5		28.2	29.5 – 33.7		31.5
	L/B	1.38– 1.53		1.46	1.43– 1.45		1.44
$P^2 - P^4$		62.0 –63.5	(2)	62.8	70	(1)	70
$M^1 - M^3$		88.0 –90.0	(2)	89.0	108.3	(1)	108.3
$\frac{P^2 - P^4}{M^1 - M^3}$		69 –72		71	65		65

* Figure in brackets indicates number of specimens in each case
** For standard deviations see Table 39

worn upper incisor, all of which could belong to a single individual. However, there is a lower RP_3 in fairly early wear and a fragment of the left side of the symphysial area with a root of LP_2 and part of a very small canine, like that in the third paratype, LT 295; these must belong to a younger individual.

Specimen LT 284 comprises two pieces of a mandible in an eroded condition and bearing only roots of some of the teeth. The larger piece belongs to the left side and is broken at the back of M_2 and anteriorly at the front of the canine. The general morphology is very like that of the second and third paratypes but the diastema between P_1 and P_2 is a little shorter. The canine has maximum and minimum dimensions within the alveolus of 24.5 mm and 19.5 mm respectively and has the shape usual in *N. tulotos*.

Specimen LT 292, which comes from the very bottom of the deltaic series, is an extremely weathered and fragile piece of a right mandibular ramus with a damaged RP_3 in moderate wear. It cannot be separated morphologically from other material belonging to *N. tulotos*, but its length of 29.9 mm and estimated breadth of not less than 24.0 mm are a little larger than usual.

SPECIMENS FROM UNIT I, MEMBER C

Material. KNM–LT 286: isolated, partially erupted RM^3. LT 293: right maxillary fragment with M^3 and damaged M^2. LT

TABLE 49. AVERAGE DIMENSIONS OF LOWER CHEEK TEETH OF *NYANZACHOERUS TULOTOS*

		Range	*N**	*S.D.**	Mean
P_1	length (L)	10.1 –11.0	2		10.5
	breadth (B)	6.0 – 6.5	2		6.2
	L/B	1.69			1.69
P_2	length	14.3 –15.5	5	0.407	15.0
	breadth	7.8 – 8.8	5	0.409	8.1
	L/B	1.74– 1.97			1.86
P_3	length	24.2 –30.0	10	2.126	27.3
	breadth	17.8 –23.6	9	1.946	20.9
	L/B	1.19– 1.44			1.31
P_4	length	22.0 –28.0	12	1.701	24.1
	breadth	19.4 –24.0	11	1.551	21.5
	L/B	1.00– 1.25			1.12
M_1	length	18.1 –22.1	8	1.388	20.2
	breadth	15.3 –17.6	7	0.985	16.5
	L/B	1.16– 1.31			1.23
M_2	length	23.0 –30.7	6	2.334	27.1
	breadth	20.3 –22.3	7	0.748	21.6
	L/B	1.05– 1.46			1.27
M_3	length	36.7 –45.5	9	2.496	41.7
	breadth	22.2 –24.5	9	0.866	23.3
	L/B	1.64– 1.97			1.80
$P_2 - P_4$		63.5 –76.0	8	4.716	69.2
$M_1 - M_3$		78.0 –98.0	7	6.439	89.3
$\frac{P_2 - P_4}{M^1 - M^3}$		0.74– 0.77	6		0.76

* *N* denotes the number of specimens in the sample; *S.D.* is the standard deviation

296: right mandibular fragment with M_2. LT 307: isolated moderately worn RM^3. LT 309: right mandibular fragment with M_3 and the roots of M_2. LT 310: left maxillary fragment with damaged P^3–M^1. LT 313: right maxillary fragment with P^3–M^3. LT 320: incomplete isolated LM^3. LT 324: fragment of maxilla with RM^3. LT 326: pieces of skull and teeth of juvenile with loose, damaged LM^2, and LM^3 (unerupted); also RI^1 in moderate wear.

Description. The foregoing account was based only on material recovered from Member B of the deltaic series. The material from Member C, above the "marker" beds, is essentially similar in structure but there may be slight differences in form and size. Comparison is made more difficult by the fact that lower teeth are commoner than uppers in the material from Member B, but the reverse is true for that from Member C. There are insufficient lower teeth for comparisons of dimensions to be meaningful, but the relative ranges and average sizes for the uppers are given in Table 48. It will be seen that the upper third molars are larger, on the average, by 4.2 mm in length and 2.0 mm in breadth, although there is some overlap in the ranges.

The only reasonably complete specimen from Member C, LT 313, has preserved all the teeth from RP^3 to RM^3 (Pl. 24), each of which is larger than in the holotype skull; the molar series is 18–20 mm longer, a difference of 20 per cent. Morphologically, however, the teeth are very similar, although the premolars have smaller cingula than those of the type, agreeing in this respect with those of the referred specimen LT 290. The same is true of the third and fourth premolars preserved in LT 310. On the other hand, the beautifully preserved RM³ in early wear (LT 324) from Member C is very closely comparable with LT 319 from the lower member. Dimensions for individual teeth have been given in the appropriate tables.

There are not enough lower cheek teeth from Member C for meaningful statistical comparisons to be made. However, average dimensions from lower cheek teeth from Member B are given in Table 49. The largest lower third molar from Member C (LT 309) is 48.8 mm long, which is about the length to be expected for a lower molar to match the uppers of LT 313 (Table 47). Apart from its larger size, however, the only point in which this lower molar differs in any way from the specimens from Member B is that, although the front of the tooth is no higher crowned, the cusps of the talonid are a trifle more hypsodont.

Although the material from Member C is too scanty to justify any definite conclusions, it does suggest that during the time represented by the deposition of the entire deltaic series of Unit 1, some increases in size were taking place.

TABLE 50. AVERAGE MEASUREMENTS OF UPPER TEETH IN FOUR SPECIES OF *NYANZACHOERUS*

	Kanam M^3	*pattersoni*	*tulotos*	*plicatus*
P^1				
length (L)			12.1	
breadth (B)			6.4	
L/B			1.90	
P^2				
length		12.1	15.3	10.5
breadth		7.4	10.7	6.7
L/B		1.64	1.44	1.57
P^3				
length		23.7	24.6	22.5
breadth		19.8	22.9	18.1
L/B		1.22	1.07	1.24
P^4				
length		19.1	20.1	18.3
breadth		22.4	26.6	20.0
L/B		0.86	0.76	0.92
M^1				
length		21.2	22.4	18.3
breadth		18.8	21.7	c19
L/B		1.13	1.03	c1.0
M^2				
length		29.7	28.7	35.4
breadth		24.9	28.1	26.3
L/B		1.22	1.03	1.34
M^3				
length	42.5	49.8	40.8	67.5
breadth	28.1	31.2	28.1	33.1
L/B	1.51	1.60	1.45	2.03
$P^2 - P^4$		55.6	60.0*	51.3
$M^1 - M^3$		98.1	91.9	121.2
$P^2 - M^3$		153.7	151.9*	172.5
$\frac{P^2 - P^4}{M^1 - M^3}$		.60	.65	.42

* Excluding P¹

THE SPECIES OF *NYANZACHOERUS*

The Four Species from East Africa

The skull characters of *Nyanzachoerus kanamensis* are not known and the skull material of *N. plicatus* is rather incomplete, although the latter exhibits features consistent with the general characteristics of the excellent skull material of *N. pattersoni* and *N. tulotos*. The skulls show some primitive features, such as the early rooting of the upper canines and the rather low-crowned cheek teeth; but they also display highly specialised characters, such as the enlarged premolars and the lateral expansion of the zygomatic arch. It is reasonable to suppose that this complex has had a fairly long geological history and diverged from the other African suid stocks well down in the Pliocene.

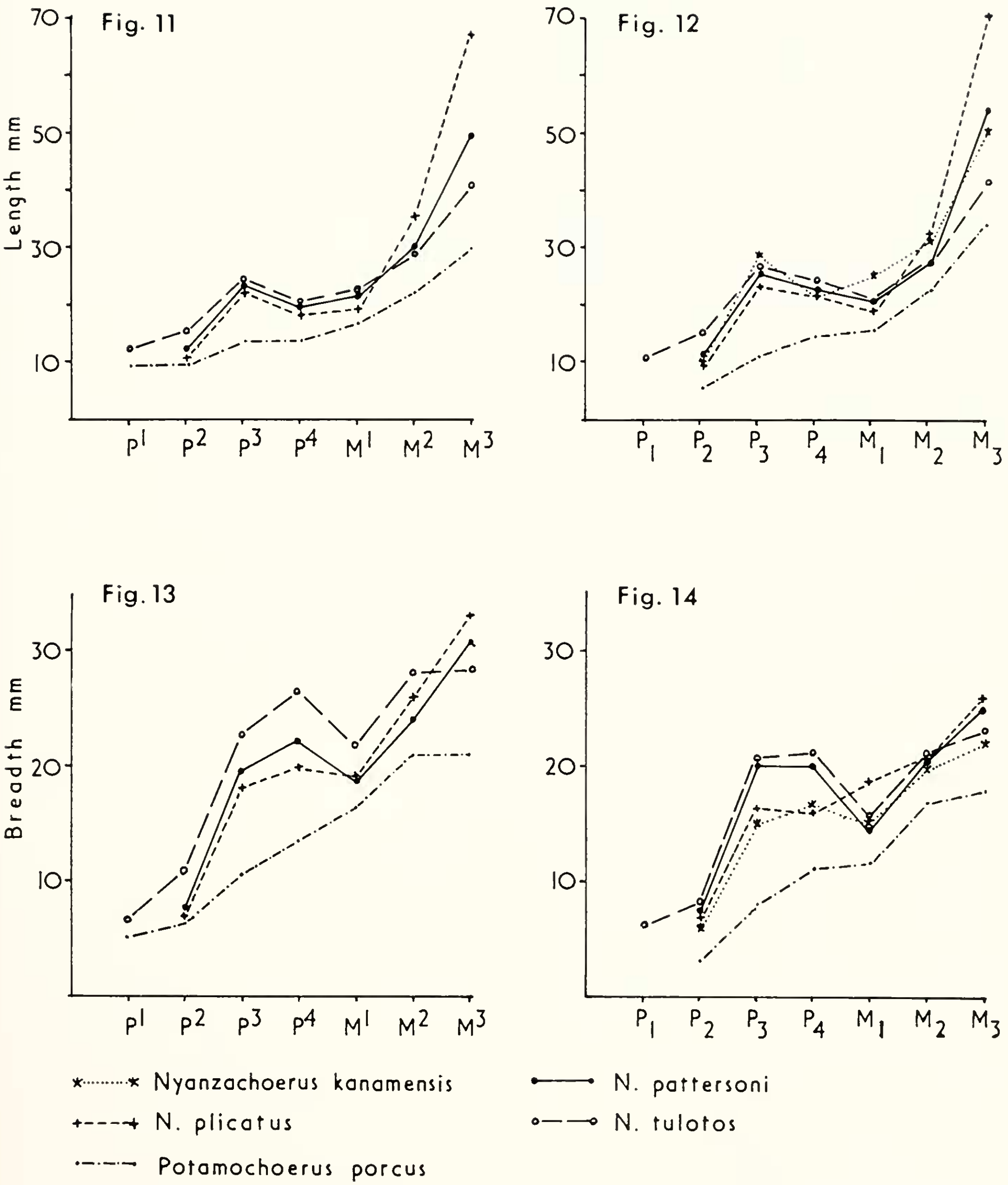
The proportions of the cheek teeth differ in the four species and an examination of these differences is useful. Tables 50 and 51 summarize the average dimensions of the upper and lower premolars and molars, and these data are presented diagrammatically in Figures 11–14 in comparison

TABLE 51. AVERAGE MEASUREMENTS OF LOWER CHEEK TEETH IN FOUR SPECIES OF *NYANZACHOERUS*

	kanamensis				
	holotype	paratype	*pattersoni*	*tulotos*	*plicatus*
P_1					
length (L)				10.5	
breadth (B)				6.2	
L/B				1.69	
P_2					
length	c10		10.6	15.0	c10
breadth	c 6		7.2	8.1	c 8
L/B	c 1.6		1.48	1.86	c 1.25
P_3					
length	28.9		25.7	27.3	23.1
breadth	15.1		20.3	20.9	16.6
L/B	1.91		1.26	1.31	1.39
P_4					
length	21.6		22.5	24.1	21.4
breadth	16.8		20.5	21.5	16.7
L/B	1.29		1.11	1.12	1.28
M_1					
length	c25		20.2	20.2	c19
breadth	c15		14.2	16.5	c19
L/B	c 1.7		1.39	1.23	c 1.0
M_2					
length	31.0	28.0	27.6	27.1	c32
breadth	20.2	19.7	21.1	21.6	c21.1
L/B	1.53	1.42	1.32	1.27	c 1.5
M_3					
length	50.5	51.0	54.7	41.7	70.6
breadth	22.0	23.2	25.1	23.3	26.4
L/B	2.28	2.24	2.17	1.80	2.68
$P_2 - P_4$	c60.5		59.0	66.4*	54.5
$M_1 - M_3$	106.5		100.0	89.0	121.6
$P_2 - M_3$	c167.5		158.0	155.4*	176.1
$\frac{P_2 - P_4}{M_1 - M_3}$	.56		.59	.75	.45

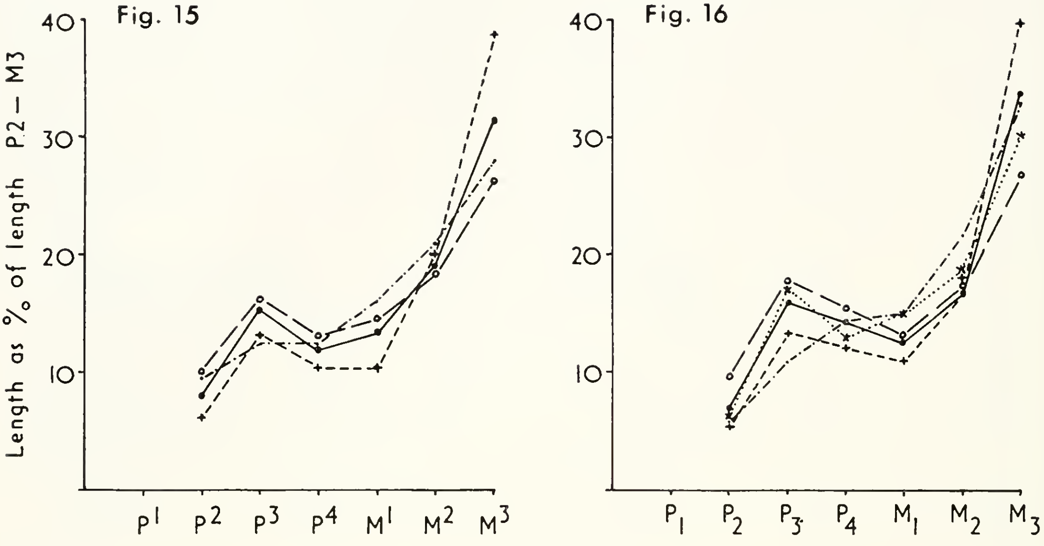
* Excluding P_1

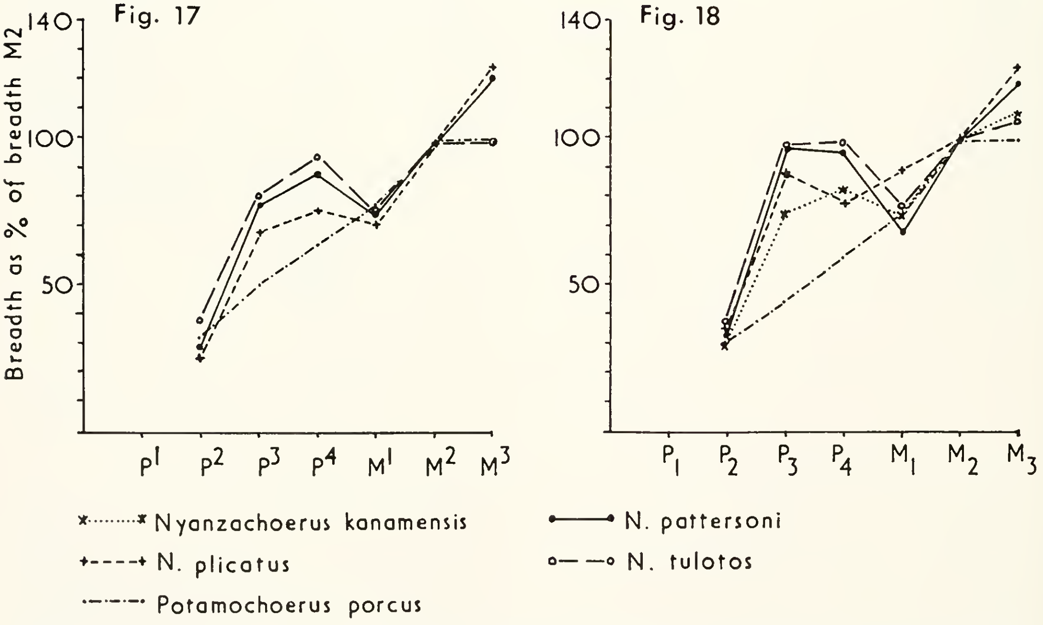
with corresponding averages for *Potamochoerus.* It will be noted that in the bushpig there is a more or less steady increase in length and breadth of the successive premolars and molars. All four of the *Nyanzachoerus* species show substantial relative elongation of the third premolar and broadening of both the third and the fourth premolars. The similarity of these trends, in comparison with a more normal suid, provides additional confirmation that the four species almost certainly belong to a single genus. Figures 15 and 16 present the data given in Table 13, in which the length of each tooth is expressed as a percentage of the total length of the premolar/molar series. This serves to emphasize the lengthening of the third premolar. Figures 17 and 18 show the data given in Table 14, in which the breadth of each tooth has been related to the breadth of the second molar as a reference standard; this is actually a



Figures 11–14. Graphs showing the variation in length and in breadth for each cheek tooth in different species of *Nyanzachoerus*, compared with *Potamochoerus porcus*. Figs. 11 and 12 show length and Figs. 13 and 14 show breadths. Figs. 11 and 13 represent the upper dentition and Figs. 12 and 14 the lower dentition.

useful practical aid in specific identification. The relative broadening of the fourth permolar is shown to be greater than that of the third premolar, as compared with the condition found in *Potamochoerus*. These diagrams also show the relative roles of the various teeth within the dentitions, indicating for *N. plicatus* a





Figures 15, 16. Graphs showing, for different species of *Nyanzachoerus* and for *Potamochoerus porcus*, the length of each cheek tooth expressed as a percentage of the total length of the series from second premolar to third molar, inclusive. Fig. 15 is for the upper dention and Fig. 16 for the lower dentition.

Figures 17, 18. Graphs showing, for different species of *Nyanzachoerus* and *Potamochoerus porcus*, the breadth of each tooth expressed as a percentage of the breadth of the second molar. Fig. 17 is for the upper dentition and Fig. 18 for the lower dentition.

considerable emphasis on the third molars and diminished weighting on the premolars; *N. tulotos* is very conservative in the molar teeth and the relative importance of the premolars is great; *N. pattersoni* has its premolars proportionally as well developed as in *N. tulotos* but the third molar is also enlarged; *N. kanamensis* is fairly similar to *N. pattersoni* but the teeth are less robust.

A possible interpretation of the dental evidence would be to suggest that a smaller and less specialised version of *N. tulotos,* with elongate but less robust premolars, might be a suitable common ancestor. *N. tulotos* itself has developed further premolar enlargement. *N. kanamensis* has not strengthened the premolars very much from this hypothetical ancestor but has elongated the third molars to a moderate degree. *N. pattersoni* has done the same, but has also developed stouter premolars. *N. plicatus,* following a somewhat different trend, has enlarged the third molar substantially and is in the process of secondary reduction of the previously enlarged premolars. However, such a relationship is still very speculative.

Probable *Nyanzachoerus* from North Africa

Material from two sites in North Africa has been referred to the Indian genus *Sivachoerus,* primarily because of enlargement of the third and fourth premolars which, at that time, was a feature known only from the Siwalik fossils. However, these specimens exhibit a number of differences in morphology from the Indian material and conform to the characteristics of the East African *Nyanzachoerus.* It is thus much more likely that they belong to this African genus, although further study of the original specimens is needed before they can be placed with assurance.

In 1936, H. Tobien described a small collection of suid material from the Wadi Natrun in Egypt and referred it to *Sivachoerus giganteus* (Falconer and Cautley). The general age of this deposit is supposedly Middle to Upper Pliocene, but there is some uncertainty about the relative dating as the total fauna has not been described. The material comprised a good part of a skull, with the palate almost complete, most of the muzzle and the parietal area, but lacking the occiput and zygomatic arches; the cheek teeth were much damaged, except for the left second and third molars. There also occur, though apparently from a different collection, an isolated right lower canine and isolated LP^3, RP^3, RP^4, LM^3 and RM_3. The skull was originally in the Geologisch-Paläontologisches Institut of the University in Freiburg, and the other specimens belonged to the Institut für Paläontologie und Historische Geologie in Munich, but they cannot now be found and are presumed to have been lost or destroyed during World War II.

Measurements are given by Tobien for the teeth, including the second and third molars of the skull, but not for the skull itself. By approximate scaling from the illustrations, the original (intact) palatal length was about 260–270 mm; the corresponding basilar length would be in the vicinity of 350–370 mm. Also by estimation from the photographs, the length of the cheek tooth series P^2–M^3 was approximately 145–155 mm. There is no indication of the presence of an upper P^1. The bony bosses surrounding the canines were only moderately developed, and, although Tobien regarded the skull as male, it might well be female. The general morphology accords fairly well with that of the holotype of *Nyanzachoerus plicatus* and is similar also to the male paratype of *N. pattersoni,* but narrower and less massive. The parietal area is not nearly as broad as in *N. tulotos.* The second and third molars of the skull have a general resemblance to those of *N. tulotos,* but the M^2 and M^3 together are longer than P^2–M^1 inclusive, which is quite unlike that species and more like the condition found in *N. plicatus.* There is thus a suspicion that the skull might represent an ancestral form of the latter. The upper and lower third molars would accord with this view. They are less like those of *N. tulotos* in being a little higher crowned and in having a more compact structure; the upper molar has a much wider talonid and is less triangular. These features would also be expected in an ancestral *N. plicatus.*

The isolated third and fourth premolars are somewhat larger than those of *N. plicatus* but are very similar in structure, lacking the "wrap around" cingula of *N. tulotos.* However, Tobien's drawings show —and he mentions in the text—strong enamel ribs on the inner (lingual) face of the main cusp, a feature seen only weakly in typical teeth of the four described species of *Nyanzachoerus.* However, there is an undescribed specimen from the Lukeino Beds in the Lake Baringo area of Kenya very similar to the Wadi Natrun material and also displaying ribbing of the upper premolar. This ribbing is supposedly typical of *Sivachoerus* and was perhaps the strongest argument for placing the material in that genus. In discussing the skull, Tobien points to a number of differences between it and the type material from India. For example, the cranial vault of *Sivachoerus* is rounded in *Sus*-like fashion, whereas in *Nyanzachoerus* it is flattened; Tobien ascribes the flattened parietal area in the Wadi Natrun skull to crushing, but it would now seem to have been inherent. He notes that the Indian genus is extremely narrow across the temporals, whereas in the Wadi Natrun fossil this region is very broad (as is typical of *Nyanzachoerus*). Another difference is in the palate, which in *Sivachoerus* has a considerable prolongation behind the third molars, but this is not the case in the fossil skull or in *Nyanzachoerus.* There is thus very little reason to maintain the generic reference of this material to *Sivachoerus.* As the Indian material does not show the zygomatic inflation so marked in *Nyanzachoerus*, as well as differing in other ways as mentioned above, it seems very unlikely that the two genera are synonymous.

Further North African material was referred to *Sivachoerus* cf. *giganteus* by Leonardi (1952), on the basis of a moderately complete skull from Sahabi in Sirtica, north-central Libya (see Appendix I). The specimen is now in the collections of the Instituto di Geologia e Paleontologia of the university in Rome, but the lower jaw described by Leonardi as a new species, *Sivachoerus syrticus*, is missing and is believed to have been destroyed during World War II. Although Leonardi's description of the skull is sound, there is a discrepancy between the dimensions given for the individual cheek teeth and the figure of 136 mm quoted for the length of the series P^2–M^3. Our measurements confirm Leonardi's individual measurements and give the length of the series as 156.5 mm on the right side and 159.5 on the left side. More complete data are given in Appendix I. The general morphology of the skull is very like the female holotype of *Nyanzachoerus pattersoni*, but the zygomatic arches flare outwards a little more and the area below the orbits is flattened. Morphologically the cheek teeth are intermediate between those of *N. pattersoni* and *N. plicatus*, but the enamel folding in the second and third molars approaches the latter more closely. It is considered that it most probably represents a form ancestral to *N. plicatus.* There is good agreement between the Sahabi specimen and the third molars from Wadi Natrun.

The lower jaw from Sahabi, now unfortunately missing, was described by Leonardi as a new species, *Sivachoerus sirticus.* He separated it from the skull on account of both the massiveness of the mandible and the presence of P_1, whereas P^1 was absent from the upper dentition. He also reports that the states of fossilization are different. In both the presence of P_1 and the general morphology of the jaw and teeth, this specimen comes close to *Nyanzachoerus tulotos*, although the symphysis is substantially longer in the Sahabi jaw; the back of the symphysis is below the back of P_3, whereas in *N. tulotos* it lies below the front of P_3. The M_2 is decidedly wider than in any of the *N. tulotos* material and M_3 is a little wider. The length of the series P_2–M_3 is given as 143 mm, which is shorter than the smallest of the Lothagam *N. tulotos* specimens. There are thus some important differences, and, as the lower teeth are rather less diagnostic than the uppers, it would be premature to suggest that *syrticus* and *tulotos* are conspecific; however, it is virtually certain that the Sahabi jaw belongs to *Nyanzachoerus*, and it may now be regarded as a distinct species, *N. syrticus* (Leonardi).

Despite the apparent improbability of there being two different species at Sahabi, one represented by a skull and the other by a lower jaw, Leonardi's reasoning is sound and must be upheld, particularly in view of the possession or lack of the first premolar. The skull appears to belong to a form similar to that from Wadi Natrun and possibly to be ancestral to *N. plicatus*, whereas the lower jaw apparently belongs to a form closer to *N. tulotos* and perhaps ancestral to it.

FUNCTIONAL ASPECTS OF *NYANZACHOERUS*

The specimens of *Nyanzachoerus pattersoni* and *N. tulotos* that have been described provide so much information about the architecture of the skull and mandible that it seems worth while attempting some analysis in functional terms. For *Nyanzachoerus plicatus,* however, the material is inadequate. As *N. pattersoni* is the species about which we have most information, it will be convenient to discuss it first and then proceed to a consideration of *N. tulotos.*

(i) *Nyanzachoerus pattersoni*

In dealing with skull architecture, an analysis of the mechanics of jaw action is important and leads to deductions about possible feeding habits. It is necessary to deal separately with the cheek teeth and with characters of the snout and incisor teeth in so far as they affect feeding methods. In the very omnivorous bushpig, rooting in the ground is a regular method of searching for food and this is reflected in the narrow snout, shovel-like symphysial region and large incisors. The forest hog and warthog are more restricted in their feeding habits, the latter feeding from choice on grass and the former on softer dicotyledonous plants. Although both can dig, neither does so as extensively as does the bushpig, and in both the snout is broader and less pointed and the incisor teeth show some reduction. In the forest hog the rhinarium is very large and rather ill-adapted for digging, but vertical wear on the tips of the lower incisors suggests that they, rather than the rhinarium, constitute the main digging organ.

In *Nyanzachoerus pattersoni,* the snout is relatively narrow, although less shovel-like than in the bushpig, and the incisor teeth are large. The wear on the tips of the teeth is such as could have been made by chewing against the upper incisors, rather than by digging. The animal therefore probably rooted in the ground as the bushpig does, but, since its adaptations to this habit are less marked, digging was probably not as important to *N. pattersoni* as it is to the bushpig.

In the extant pigs, as might be expected from their diets, the cheek teeth of the warthog are the most specialised and those of the bushpig the least specialised for grinding; the same is true of their jaw movements. In the bushpig the jaw action is mainly a simple crushing with a slight rotatory movement in which the sideways component is not much more important than the fore-and-aft motion. In the forest hog the sideways component of the movement predominates, while in the warthog the movement is almost exclusively sideways and the fore-and-aft component is negligible. These differences are reflected in the character of the glenoid, which is a narrow, almost flat bar in the warthog and is wider and slightly more concave in the other two species: it is also shown in the relative size of the temporalis muscle, which is responsible for pulling the jaw backwards.

The size of the temporalis relative to the superficial masseter may be expressed in terms of the lengths of their origins on the skull. If the temporalis is measured from the tip of the postorbital process to the posterior end of the temporal crest, then the ratio of this to the length of the masseter insertion along the lower margin of the zygoma gives a measure of the relative importance of the temporalis muscle; this, in turn, is a measure of the relative importance of the back-and-forth component of the jaw action. For the extant species the temporalis:masseter ratios are about 90 per cent for bushpig, 65–70 per cent for forest hog, and less than 50 per cent for warthog.

The cheek teeth of *N. pattersoni* are only slightly hypsodont, and, although ultimately they are abraded to a flat surface, in early wear stages some similarity to the wear on *Hylochoerus* teeth is apparent. In no specimen can the lengths of both masseter and temporalis origins be measured, but in the female skull, the restoration necessary to provide these measurements can be made with a fair degree of confidence. Working from the restoration, maximum and minimum estimates for the temporalis:masseter ratio are 78 per cent and 65 per cent. Both values are well above the figures for warthog, possibly a little more than is typical of *Hylochoerus* but distinctly below those for bushpig. This, together with the slightly narrowed glenoid suggest that, as in *Hylochoerus*, there has been some reduction in the importance of the fore-and-aft component in the jaw movement.

The character of the posterior margin of the angle of the mandible remains to be considered. This resembles the potamochoeroid condition and the angle lacks the widening found in both *Hylochoerus* and *Phacochoerus*. As explained elsewhere (Ewer, 1970) this widening is interpretable as an adaptation to withstand the strains produced when the superficial masseter and internal pterygoideus muscles contract alternately rather than synchronously, in the manner required to produce an efficient sideways grinding action. Its absence in *Nyanzachoerus pattersoni* shows that although there has been some elaboration in the third molars, increasing the surface area and the lasting power of the dental battery, specialisation in the pattern of muscular contraction involved in chewing has not yet occurred—or at least must be at such an early stage that skeletal adaptations to the complex asynchronous contraction sequence have not yet been acquired.

It has been argued elsewhere (Ewer, 1960) that, on general grounds, one would expect elaboration of the teeth to lead the way in evolution, and specialisation of jaw action to follow only when the teeth have reached a stage of complexity making the sideways grinding action "worth while." The adaptational syndrome shown in *N. pattersoni* appears to be in accord with this view. In terms of feeding habit, the characters of the skull and jaws of *N. pattersoni* appear to imply a diet in which roots and tubers are less, and green vegetation correspondingly more, important than they are in the bushpig; the degree of grinding ability shown, however, does not appear sufficient to cope with a diet in which abrasive grasses predominate, as they do in that of the warthog. The adaptations shown in the dentition and chewing mechanism thus appear to be related to an increasing dependence on browsing or grazing on surface vegetation, which requires efficient trituration, and a corresponding decrease in the importance of soft bulbs and tubers, which must be dug up but require relatively little grinding.

It is not, however, these characteristics of dentition and jaw muscles that constitute the most striking feature in the *Nyanzachoerus pattersoni* material but rather the structure of the zygoma. The variability in the development of the zygomatic knobs has been described and has been interpreted here as resulting from sexual dimorphism. If we assume this to be correct, the significance of the knobs still requires elucidation. Their position and their greater development in the male than in the female at once invite comparison with the zygomatic warts of *Phacochoerus*. In the earlier paper (Ewer, 1958) it was suggested that although these warts may have originated with a protective function, their present degree of elaboration is explicable only if they act as display organs. Geist (1966) has expressed the same opinion.

Mammalian offensive threats are most commonly derived from intention movements of attack (Ewer, 1968). This automatically produces a "weapon threat," in which the opponent is given a view of the organs to be used in the attack that may follow. The warthog's method of fighting, described by Frädrich (1965), makes it virtually certain that the function of the warts is to increase the intimidatory effect of a threat display. In fighting, warthogs adopt a forehead-to-forehead pushing technique, very similar to the type of contest characteristic of the horned and antlered artiodactyls. The broadness of the forehead makes a pushing contest of this type possible even in the absence of locking horns or antlers; the large upper tusks, too, may help to compensate for this lack and may also act as holding organs, ensuring that the contestants' heads do not slip apart. In the narrow-headed, short-tusked bushpig, the danger of slipping is minimised by the animals turning their heads slightly sideways, so that they cross snouts, instead of making a symmetrical forehead-to-forehead contact. In the warthog, it is thus the broad forehead, rather than the tusks, that constitutes the main weapon. The intention movement for warthog fighting is therefore to face the opponent and lower the snout, so that this "weapon" is displayed. The zygomatic warts are so placed as to be visible to the opponent and have the effect of increasing the apparent width of the head, which is equivalent to making their possessor appear more dangerous.

In *Nyanzachoerus pattersoni*, the broad forehead suggests that fighting must have been of the warthog type and the zygomatic knobs, like the warts of *Phacochoerus*, are so placed as to increase the width of the head displayed to an opponent in the "ready for action" position. The most plausible suggestion as to their function is therefore that they constitute display organs, used in intraspecific contests between males.

In *Phacochoerus* the zygoma underlying the wart is somewhat inflated and there is a roughened area directly beneath the wart. The knobs of *Nyanzachoerus*, on the other hand, show no such roughening and one must therefore conclude that in life they were not surmounted by any specialised epidermal thickening. Selective pressure for increasingly impressive threat would thus appear to have produced the same effect in the two cases by rather different means. In *Nyanzachoerus* head width is increased by bony outgrowths, in *Phacochoerus* the same result is attained by epidermal thickenings. The latter would appear to be the more satisfactory arrangement, since not only are warts lighter than bony knobs (even though the latter are hollowed out inside) but their growth does not increase the demand for calcium, and any damage to them is likely to have much less serious consequences than would an injury to bone.

Geist (1966) makes a further point with reference to the horned and antlered artiodactyls. In some species these weapons show sustained positive allometric growth, and, even after maturity is reached, the age of an animal is manifested in the relative size of the horns or antlers. In other cases this is much less marked and once the adult body proportions are attained, there is little further change. Geist relates this difference to differences in the social organisation of the various species. The same considerations would apply to the zygomatic protuberances of *Nyanzachoerus.* Thus, if sufficient material becomes available, it is possible that the growth characteristics of the zygomatic protuberances may ultimately provide the basis for deductions about social life.

Two final points may be made. In living species visual displays are not usually important in the behavior of animals that are nocturnal or that live in dense cover; the knobs of *Nyanzachoerus* therefore suggest that this species was probably diurnal and lived in terrain that was at least moderately open. Secondly, it should be noted that in extant mammals, fights between males are normally intraspecific and members of a different species are not molested. One might therefore expect that if zygomatic knobs were evolved in other species sympatric with *Nyanzachoerus pattersoni,* these would have some visible differences, making it easy for the animals to tell a conspecific male from one belonging to another species. Although one might expect such differences to take the form of differences in the shape of the knobs, it should be remembered that even similar knobs would appear different in life, if surmounted by hair tufts of different colours.

(ii) *Nyanzachoerus tulotos*

As far as the characters of the dentition and feeding methods go, interpretation of the skull of *Nyanzachoerus tulotos* presents no particular difficulties. The incisor region of the snout is essentially similar to that of *N. pattersoni,* but possibly a little more elongated. The snout was almost certainly an efficient digging organ, although not as highly specialised for this function as that of the bushpig. The cheek teeth resemble those of *N. pattersoni* but are more primitive, the third molars being short-crowned and less elongated. The characteristics of the glenoid, of the mandibular angle, and of the wear facet on the lower canine suggest a relatively primitive jaw movement, without the development of a specialised sideways grinding action. It would thus seem that *N. tulotos,* like *N. pattersoni,* was a mixed feeder in the process of becoming adapted to a more abrasive diet requiring efficient trituration with the cheek teeth. *N. tulotos*, however, is at an earlier stage and its masticatory adaptations are less advanced.

It is, however, in interpreting those characteristics of the skull of *N. tulotos* that are not related to feeding that problems arise. The anterior and posterior parts of the skull are sharply contrasting. The muzzle, with its enlarged maxillary flanges, premaxillary thickenings, and thick preorbital ridges, is heavily built and rugged. The broad frontal and parietal region, on the other hand, is devoid of any bony ridges or protuberances: its unusual width is produced by overhanging flanges of the frontals and parietals that are thin and delicate by comparison with the muzzle region. The thickening along the line of the parietal and occipital crests characteristic of *Hylochoerus* is completely absent. All this suggests that *N. tulotos* probably fought by pushing with the snout, rather than the forehead, more after the manner of the bushpig than the warthog or forest hog. If it adopted the bushpig snout-crossing tactic, then the preorbital ridges and premaxillary thickenings would have acted as anti-slip devices, preventing the opponent's snout from slipping either upwards cranially or downwards rostrally.

The ease with which a frontal fighting technique may lead to the evolution of structures increasing the effectiveness of frontal threat has already been discussed in relation to *Nyanzachoerus pattersoni.* The same consideration would apply here and the zygomatic protuberances of *N.*

tulotos, like those of *N. pattersoni*, can be interpreted as threat organs. The characters of the frontal and parietal region of the skull of *N. tulotos*, however, suggest a further possibility. The widening of the skull table does not appear to relate to a forehead pushing-fighting technique and it is certainly not the result of any enlargement of the braincase. It therefore seems possible that the widening of the forehead, as well as the zygomatic exaggeration, is an adaptation whose function is to increase the intimidatory effect of frontal threat.

It is, of course, possible that once a broad forehead has been evolved, a transition to a forehead contact in fighting might follow. With this technique, the combatants go over directly from threat to attack in a symmetrical manner and there is less chance of their heads slipping apart than in the snout pushing technique, which requires the opponents, as they meet, to turn their heads to opposite sides so as to cross snouts. Slipping apart of snouts, of course, involves the danger of a slash with the sharp lower tusks. The primary function of the maxillary flanges appears to be to protect the tendons of the snout muscles against a wound of this sort.

If snout pushing is replaced by a forehead to forehead contact in fighting, then a new set of selective pressures comes into operation: thickening and strengthening of the forehead becomes a desideratum and possibly also the production of ridges to minimize the chance of slipping. In fact, the broad forehead, which began as a deceptive intimidatory device, must be converted into a genuine weapon. At the same time, the importance of the maxillary flanges and the thickening on the muzzle declines. One might therefore expect to find the evolution of the fighting forehead accompanied by reduction in the fighting adaptations of the snout.

It does not, of course, follow that forehead contact is always secondary and must necessarily be derived from a snout-crossing fighting technique nor that all lineages have followed the same evolutionary course. If a frontal technique is adopted then the forehead, if it is not too rounded, rather than the muzzle, might become the main contact area right from the start. One would not, however, expect that the inherently more effective forehead contact would ever be replaced subsequently by snout-crossing.

Unfortunately, in none of the specimens of *N. pattersoni* is the vertex of the skull well preserved. It is therefore not possible to say whether adaptations increasing the efficiency of the forehead fighting had been evolved in this species. It is, however, clear that the muzzle is much less specialised for snout-crossing than that of *N. tulotos*, and it is tempting to regard the smaller maxillary flanges and preorbital ridges of *N. pattersoni* as being secondarily reduced, rather than merely less developed than those of the latter. Such a view is in accord with the more advanced characteristics of the dentition of *N. pattersoni*. While we do not wish to suggest that *N. tulotos* is itself directly ancestral to *N. pattersoni*, they do appear to represent two closely related species, one of which is more primitive than the other in its fighting technique and associated structural adaptations, as well as in its dentition and feeding adaptations.

OTHER SUID REMAINS FROM KANAPOI

Nyanzachoerus sp.

There are three specimens that seem to belong to *Nyanzachoerus* but which are difficult to place. Although the teeth are closer to those of *N. pattersoni* than to those of *N. plicatus*, they cannot be matched exactly by any of the other material that has been assigned to these species. The specimens may be considered individually.

KNM–KP 218 comprises fragments of a left mandible in which the bone is much blackened and unlike nearly all the other

TABLE 52. DIMENSIONS OF TEETH OF *NYANZACHOERUS* SP. IN MANDIBLE FRAGMENT KP 218

Tooth	Length	Breadth	Height
LP_3	20.0	13.8	13 +
LP_4	21.6	15.4	14.7+
LM_3	32.7 + (c50)	21.5 + (c25)	20 +

TABLE 53. DIMENSIONS OF UPPER TEETH OF *NYANZACHOERUS* SP.

Specimen No.	Tooth	Length	Breadth	Height
KP 214	LP^3	21.4	18.5	11.5+
"	LP^4	17.8	19.0	11.5+
KP 211	RP^3	18.7	17.5	8.5+
"	RP^4	16.3	19.5	9.0+

material from Kanapoi in this respect. By contrast, the teeth are grey, whereas many of the other Kanapoi teeth are black, so there exists a possibility that the specimen was not in place but was derived from some other deposit in the vicinity. Preserved are LP_3 and LP_4 in moderate wear, a little worn LM_3 lacking the anterior pillars, a fragment of an M_2, and a small piece of canine. Measurements are given in Table 52. Although the M_3 is essentially similar to the corresponding tooth in *N. pattersoni,* the two premolars are a good deal narrower than in any of the undoubted *N. pattersoni* material; however, the LP_3 is shorter than the LP_4, contrary to the situation in all the other known *Nyanzachoerus* material, and particularly unlike *N. kanamensis.* Nevertheless, P_3 is larger than in normal suid dentitions, where it is usually only about 60–70 per cent of the size of P_4. The scrap of M_2 is not very helpful but its structure is not readily matched in any genus other than *Nyanzachoerus.* The canine fragment also shows clearly the rather U-shaped cross section typical of this genus. The evidence thus points towards the assignment of the specimen to *Nyanzachoerus;* its specific status is problematical but it is not impossible that it may be an unusual variant of *N. pattersoni.*

KNM–KP 214 is a fragment of left maxilla retaining the fairly well worn LP^3 and LP^4. Measurements are given in Table 53. Morphologically these teeth are very similar to the corresponding molars in the holotype skull of *N. pattersoni,* but the cingulum development in the LP^3 is weaker and the shape of the crown suggests that the teeth were originally less hypsodont than in the holotype. The P^3 is at the lower limit of size and P^4 is narrower than in any known specimen of *N. pattersoni.* These features are like those of the lower teeth in KNM–KP 218 and similar conclusions apply to it.

KNM–KP 211 is a piece of right maxilla with very worn RP^3 and RP^4, the crowns of which are almost patternless. The dimensions are smaller than those of KP 214 (see Table 53), but the relative size of the P^3 suggests that the specimen may belong to a small *Nyanzachoerus;* its reference is problematical.

Genus *NOTOCHOERUS* Broom 1925

Notochoerus cf. *capensis*

Notochoerus capensis Broom, 1925: 307, text-fig.

Remarks. The status of *Notochoerus capensis* will be discussed elsewhere and some comments on the differences between that species and the Kaiso *Notochoerus euilus* have been given (Cooke and Coryndon, 1970). Accordingly, it is not proposed to repeat here the full details and synonymy relating to this giant extinct pig, especially as there is uncertainty about the proper specific designation for the Kanapoi material. An undescribed partial skull from the lower Omo beds exhibits some of the features seen in the Kanapoi material and this specimen is tentatively regarded as *Notochoerus* cf. *capensis,* as is also the bulk of the material from Laetolil described by Dietrich (1942) as *Hylochoerus euilus.* The Omo skull is a good deal smaller than the Kanapoi form and it is unlikely that the two are specifically identical. In all probability the Kanapoi form belongs to a new species but the specimens are not considered adequate as type material, despite the novel features they display.

Material. KNM–KP 226: incomplete mandible, retaining RP_3 and imperfect RM_3. KP 241: much damaged mandible with RP_3. KP 242: skull fragments associated with KP 241. KP 267A: fragment of lower jaw with LM_3. KP 267B: fragment of lower jaw with RP_3 and RP_4. KP 267C: left upper canine, lacking the tip. KP 210: fragment of lower jaw with rolled and damaged RM_3.

DESCRIPTION

Specimen KNM–KP 226 consists of the greater part of a mandible, which is exceptionally massive. The symphysial area is well preserved but the two rami are severely crushed and the back of the mandible is missing. On the right side the outline of a good deal of M_3 is still visible, broken off at the talon, but the only tooth which is intact is the right P_3. This latter tooth is 22 mm long, 14 mm wide, and 8 mm high. It seems to consist of a single stout cone and has no anterior cingulum; the back is broken and it cannot be determined whether a cingulum was present or not, but there is no sign of any posterior cone. The socket for the fourth premolar is fairly small and the entire premolar series was no more than 42 mm long. The first and second molars together occupied about 37 mm, and the third molar exceeded 75 mm in length.

The symphysis extends back almost as far as the front of the third premolar and is exceptionally long, measuring 186 mm from the front of the jaw between the sockets for the large central incisors. The distance from the front of the mandible to the estimated position of the back of the third molar is 355 mm, and it is estimated that the length of the entire mandible must have been in the vicinity of 50 cm (compared with 35 cm for a very large *Hylochoerus*). The front of the mandible flares outwards and the width at the back of the canines, as preserved, is 175 mm and was probably a little greater; this is almost double the width in a male *Hylochoerus.* The general shape of the symphysis is similar to *Hylochoerus* or *Phacochoerus,* but all six incisors were retained and the front of the jaw is even less curved than in the forest hog. The angle at the back of the symphysis lies a little below the lower border of the rami and the profile is thus more phacochoerine than hylochoerine. The sockets for the incisors are filled with matrix. The central incisors are compressed and are flanked by much larger and more equidimensional teeth. There is no socket for a lateral incisor on the right side and only a small one on the left. The left canine is still in place, although broken off in line with the incisors. It has an almost U-shaped or rounded triangular transverse section with the greatest diameter 39 mm and the transverse diameter 27 mm. A detached piece of this canine is also associated with the jaw and it shows a trace of the bottom of an anterior wear facet. The jaw is illustrated in Plate 26.

Specimen KP 241 is a much damaged mandible without any cheek teeth except the right P_3 (Pl. 26). This tooth consists of a stout main cone, a very minute anterior cusp, and a fairly narrow posterior cingulum. The socket for a small P_2 is present. The canines are exposed in cross section in the broken symphysial area and are a little larger than those in the other specimen (Pl. 26; Figure 19). The symphysis was about 185–190 mm long, but does not seem to have been quite as wide across the canines as is the case in KP 226. A fragment of the back of the RM_3 is preserved in a detached portion of the mandible that does not quite join the remainder. It is in advanced wear and shows the back of the last pair of lateral pillars and a complex of six enamel islands forming the talonid.

The third fragment of lower jaw, KP

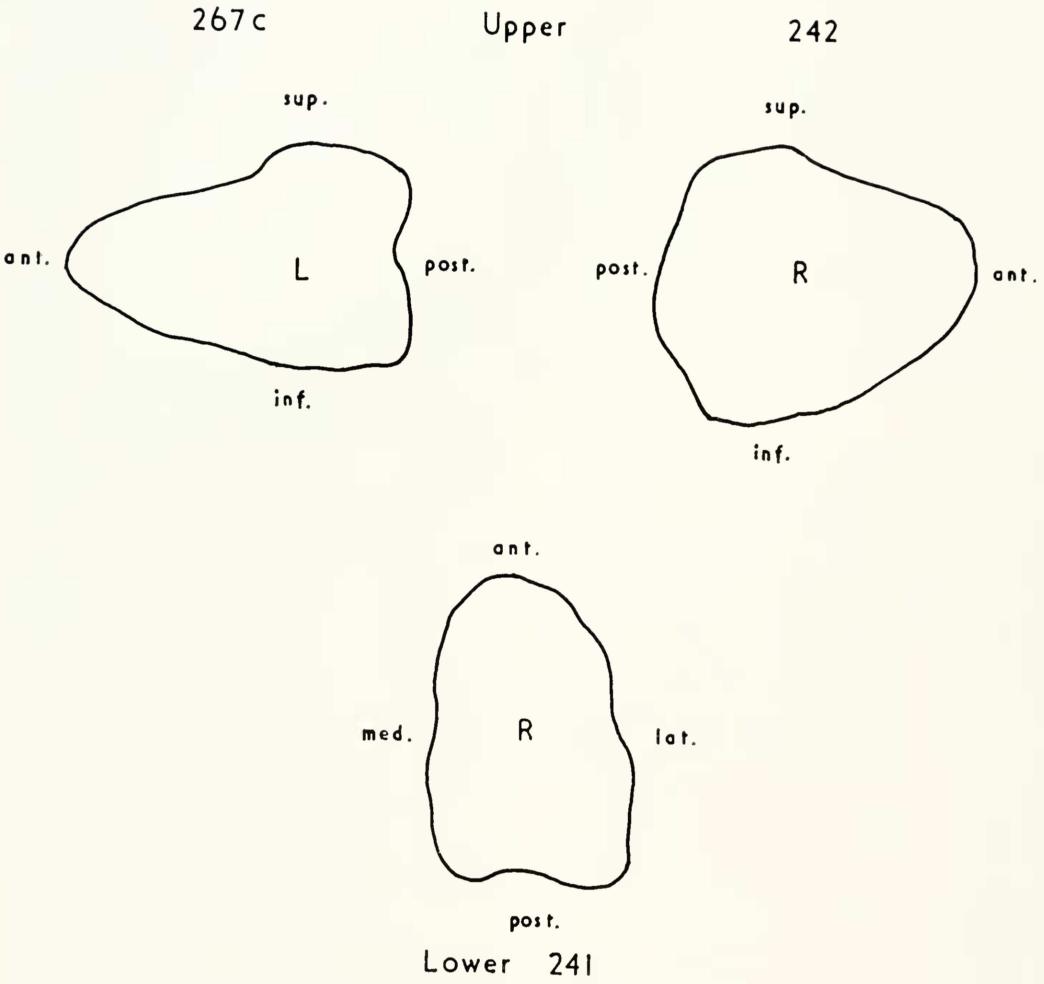


Figure 19. Sections of upper and lower canines referred to *Notochoerus* cf. *capensis* from Kanapoi. Nat. size. Abbreviations as in Fig. 5.

267A, matches the other specimens in contour and massiveness but has only the LM_3 preserved. This is in very advanced wear and its dimensions are 82 mm long, 29 mm broad and 8–9 mm high. The tooth originally had three well-developed pairs of lateral pillars, a weaker pair behind them, and a complex of four or five pillars in the talonid. Accessory columns existed at the base between the lateral pillars on the buccal side. As far as can be determined, there was only a single median pillar between successive pairs of laterals. The tooth is illustrated in Plate 26.

There is also a fragment, KP 267B, containing the right P_3 and P_4. P_3 is 22 mm long, 13.5 mm broad, and 13.5 mm high. It is a little narrower than the two corresponding teeth in the other jaw. There is no sign of an anterior cusp and the posterior cingulum is small. P_4, which is heavily worn, is 19 mm long and 16 mm broad. It appears to have consisted only of a single stout cone. With it was associated a large upper canine with the tip missing (KP 267C). The length, measured in a straight line across the arc, is 27 cm. At the base the tusk is 47 mm by 32 mm, while at the broken tip its dimensions are 38 mm by 22 mm. In cross section it tends to be trapezoidal with the posterior face perpendicular to the broad lower face, a narrow dorsal face parallel to the lower one, and a sloping anterior face; it is shown in Figure 19. This cross section, which might be described as a highly distorted bell-shape, is characteristic of upper canines from other sites that have been ascribed to *Notochoerus;* in some of these the "bell-shape" is more marked.

Specimen KP 210 consists of a fragment of right mandible with a rolled and damaged third molar preserved. The tooth is 81 mm long and 28 mm broad anteriorly. There are three well-developed pairs of lateral pillars, separated by single median columns, a much weaker fourth pair of lateral pillars, and a complex of three pillars in the talonid. The pattern in wear is very like that of lower teeth from Omo that have been assigned to *Notochoerus euilus,* but the Kanapoi specimen is more robust and the fourth pair of lateral pillars is much weaker. The talon is little worn and the original crown height can be estimated as about 30 mm.

Associated directly with the mandible KP 241, and numbered KP 242, is a collection of small skull fragments. It has been possible to assemble only a few pieces, but these include most of the front of the palate with the bases of the canines, and also a detached large bony knob from the zygoma. The front of the palate was shaped very much like that of *Hylochoerus,* but about half as big again, and the canines themselves and the bony flanges around their bases are proportionally larger than in the forest hog. The canines are rounded triangular or subtrapezoidal in shape and the dimensions of the right canine in the alveolus are: transverse diameter—42 mm, dorso-ventral—36.5 mm. A similar shape is seen in canines of *Notochoerus euilus* in a skull from Omo (not yet described), and the morphology of the palate is also similar except that the canines are directed slightly more forwards in the Kanapoi than in the Omo specimen. The Kanapoi fragments also show that the anterior cheek teeth are less reduced than in the Omo species.

The bony knob mentioned above represents a protuberance on the zygomatic arch, rather different in nature from the expanded zygoma of *Nyanzachoerus.* It is almost cylindrical in form, expanding slightly near the broken base where it joined the more normal part of the zygoma; the other end is rounded and slightly rugose. It could, perhaps, best be described as thimble-shaped. The "height" (lateral extent) is 118 mm, and the diameter of the subtriangular cylinder is 85–95 mm. A very similar, but smaller, protrusion occurs on the zygoma of an undescribed skull from Omo, also provisionally referred to *Notochoerus* cf. *capensis.* The Kanapoi "knob" and the Omo skull are shown in Plate 27.

DISCUSSION

This collection, unsatisfactory as it is, establishes the existence of a very large suid with some distinctive characteristics, apart from its absolute size. The form of the mandible is hylochoerine or phacochoerine, with a long symphysis. The lower incisors have a normal complement of six, but show reduction in size both in the central and in the outer lateral pairs. The large lower canines are U-shaped to subtriangular in cross section and the upper canines are trapezoidal to a squashed bell-shape in cross section. The premolars are reduced, with P_2 very small and the whole premolar series only about half the length of M_3 alone, M_3 itself being about half of the total length of the cheek tooth series. The cheek teeth, although large, are apparently small in relation to the great size of the skull, bearing about the relationship seen in *Hylochoerus.* A large cylindrical protuberance occurs on the zygoma, possibly restricted to male animals.

Notochoerus cf. *euilus*

Hylochoerus euilus Hopwood, 1926: 21, text-fig. 7, pl. 2, figs. 7–10.
Notochoerus euilus Leakey, 1958 (in part): 31.
Notochoerus euilus Cooke and Coryndon, 1970: 147, pl. 7, figs. 7–10.

Remarks. The status of the type material of Hopwood's species from Kaiso has been considered elsewhere (Cooke and Coryndon, 1970). The lower molars are fairly elongate but relatively narrow, measuring about 65–75 mm by 25 mm, and are not very much higher crowned than their width. They normally have four pairs of laterals in the lower third molars, plus a small talonid or talonid complex. The lateral pillars are well separated for most of their height and they wear to produce enamel islands with a dumbbell or distorted H-shape, becoming collar-stud-shaped in advanced wear. Similar teeth occur plentifully in the lower part of the Omo beds, but are undescribed, and are associated with mandibles, upper dentitions, and a skull. The lower and upper canines are similar in general structure to those described above for the *N.* cf. *capensis* material from Kanapoi; the presumed *euilus* skull lacks the zygomatic knobs and differs in other respects from the Omo skull regarded as cf. *capensis.*

DESCRIPTION

One incomplete lower third molar KNM–KP 245, does not fit well with the material ascribed to *Notochoerus* cf. *capensis* above, but agrees well with the material from the lower Omo beds regarded as belonging to *N. euilus.* As preserved, the specimen is 44.5 mm long and it was probably near 65 mm when complete. It is 25 mm broad at the base of the crown and the height is 29 mm on the little worn posterior column and may have been as much as 35 mm when intact.

Another specimen, KP 209, is a chemically corroded fragment of a lower third molar showing characteristics similar to those of the Omo *N. euilus.*

Also in the Kanapoi collection are a rather slender left lower canine (KP 248) and the broken tip of a similar tusk (KP 224). The almost complete specimen is 128 mm in length from the tip to the broken root area; the greatest diameter at the base is 23 mm and transversely is 17.5 mm. There is a wear facet on the upper 4 cm of the tusk. All three sides of the triangular tooth are coated with enamel that is thickest on the buccal side. There is a fairly deep posterior groove in the complete specimen, but this groove is shallower in the broken tip of KP 224. While it is not impossible that these tusks belonged to a variety of *Nyanzachoerus,* it is difficult to place them at the present time.

OTHER SUID REMAINS FROM LOTHAGAM

Nyanzachoerus sp.

Two specimens, one from below the "marker" horizon in Unit 1 and one from a level towards the top of Member C, are difficult to place within the known range of *Nyanzachoerus tulotos,* although it is not completely impossible that they may belong to variants of that species.

Specimen KNM–LT 318, from the lower horizon, consists of parts of the two mandibular rami. The left is broken behind LM_3 and through the symphysis a little in front of the root of LP_2, exposing the canine; part of the right corpus joins the back of the left posterior border of the symphysis and is broken off behind RM_2. On the left side, only M_3 is preserved, although damaged anteriorly, but the roots of the other teeth are still present, broken off at the alveolar margin. On the right side, part of the battered crown of P_3 remains, as well as the extremely worn RM_2. The RP_3 is a little larger than the biggest specimen assigned to *N. tulotos* and seems to have

TABLE 54. MEASUREMENTS ON MANDIBLE LT 318 FROM UNIT 1, MEMBER B

Tooth	Description	Length	Breadth	Height
LP$_2$	Roots only	17.0	10.0	–
LP$_3$	Roots only	34.0	28.5	–
RP$_3$	Damaged crown	28.7 + (31e)	23.7 + (24e)	10.0+
LP$_4$	Roots only	31.5	31.0	–
RP$_4$	Roots only	32.5	32.5	–
LM$_1$	Roots only	21.5	22.0	–
RM$_1$	Roots only	20.0	21.6	–
LM$_2$	Roots only	27.0	24.5	–
RM$_2$	Very worn crown	24.7	21.6	dentine
LM$_3$	Damaged crown	39.5	23 e	10.8+

only a very weak anterior cingulum. The RP$_4$ is shown by the roots to have been substantially longer than any of the other known specimens, but it is also very much wider so that the crown must have been more or less equidimensional. By contrast, the LM$_3$ is particularly small, lying at the lower limit of size for *N. tulotos.* The canine is of moderate size, with a maximum diameter of 25.0 mm and a minimum of 20.3 mm, and its shape is subtriangular like that of *N. tulotos.* Dimensions for the cheek teeth and the roots are given in Table 54 and the specimen is shown in Plate 28. Although it is possible that splaying of the roots could have the effect of exaggerating the apparent size of the missing crowns of the premolars, the appearance of the jaw suggests that the specimen belongs to a different species showing further premolar enlargement beyond that displayed in *N. tulotos.*

Specimen LT 299, from Member C, is an isolated left P$_3$ in moderate wear. The dimensions are: length 29.6 mm, breadth 24.7 mm, and height 20.3 mm. Like the corresponding tooth in the mandible from the lower horizon, it differs from normal *N. tulotos* in being broader and in having only a very faint anterior cingulum and no anterior cingular cusp.

Nyanzachoerus cf. *pattersoni*

Five specimens from Lothagam seem to belong to a *Nyanzachoerus* different from *N. tulotos* but close to *N. pattersoni.* Two are from the upper part and three from the lower part of Unit 1.

UNIT 1, MEMBER B

KNM–LT 312: a piece of right mandibular ramus with pieces of P$_4$, M$_1$ and M$_2$, the dimensions of which are very close to those of LT 294 (below), as is also the morphology of the tooth fragments that remain. This specimen is recorded as coming from the very base of the deltaic series, although it is a surface find and its provenance is not certain.

LT 294: a piece of left mandibular ramus with P$_4$ and M$_2$ intact, but only the roots of M$_1$ (Pl. 29). The teeth are very little worn and show the typical features of *Nyanzachoerus.* The LP$_4$ is 22.6 mm long, 17.3 mm broad, and 22.5 mm high. Although it is almost the same size as the P$_4$ in the type of *N. kanamensis,* and thus narrower than is usual in *N. pattersoni,* it is morphologically much closer to the latter species. The LM$_2$ is much shorter than in *N. kanamensis* but agrees very well with *N. pattersoni;* its length is 26.8 mm, breadth 20.0 mm, and height as preserved 15.5 mm. The specimen probably represents an early *N. pattersoni.*

LT 304: a fragment of left maxilla with roots of parts of P^3 and M^2, part of an extremely worn M^1, and the buccal half of P^4. The general morphology of the pieces of maxilla, which show the beginning of the zygoma, and also the size and form of the tooth roots and enamel remnants, resemble the corresponding parts of the holotype skull of *N. pattersoni*. Identification is very uncertain.

UNIT 1, MEMBER C

LT 285: two associated specimens are an upper right M^2 in fairly advanced wear, and a piece of left mandibular ramus with most of P_4 and the three molar teeth; M_1 is worn to dentine only and M_2 has some enamel remaining. The dimensions are given in Table 55 and the ramus is shown in Plate 29. The teeth are near the upper range of size variation for *N. pattersoni*, but the morphology is typical and there can be very little doubt about the identification.

TABLE 55. DIMENSIONS OF TEETH OF SPECIMEN LT 285 REFERRED TO *NYANZACHOERUS* CF. *PATTERSONI*

Tooth	Stage of wear	Length	Breadth	Height
RM^2	Advanced	30.0	27.8	8.0+
LP_4	Fairly advanced	–	21.3	12.0+
LM_1	Extreme	16.8+	c16	dentine
LM_2	Very advanced	29.7	23.0	8.0+
LM_3	Moderately advanced	57.2	26.0	15.3+

Nyanzachoerus plicatus

Three specimens from the upper part of the Lothagam succession are assigned to this characteristic Kanapoi species. Two are from the uppermost part of Unit 1, Member C, higher than any of the *N. tulotos* material; one specimen comes from the fluviatile deposits of Unit 3, well above the intrusive basalt (see Fig. 2).

TOP OF DELTAIC SERIES (MEMBER C)

KNM–LT 311: this is an isolated upper third molar in early wear, damaged anteriorly so that the front buccal pillar is lost and the lingual pillar is only partially preserved. The present length is 57 mm and is estimated as having been close to 70 mm when the tooth was intact; the breadth is 34.1 mm and the height of the little worn second lateral pillar on the buccal side is 26.5 mm and that of the unworn third lateral pillar on the lingual side is 27.6 mm. The form and structure of the tooth is characteristic of the species, but it is a little broader and slightly less hypsodont than the typical Kanapoi material.

TABLE 56. MEASUREMENTS ON DAMAGED TEETH LT 308 FROM TOP OF UNIT 1, MEMBER C REFERRED TO *NYANZACHOERUS PLICATUS*

Tooth	Length	Breadth	Height
RP_3	29.0	21.0e	24.5+
RP_4	25.8	14.5 + (c22)	20.5+
RM^2	34.1	24.0	12.0+
left lower canine		maximum 39.0	minimum 27.0

KNM–LT 308: this collection apparently represents the remnants of a disrupted skull and comprises a piece of lower left canine, an imperfect RP_3, the buccal half of RP_4, an incomplete RM^2, and a scrap of RM^3. The dimensions are given in Table 56. The lower premolars are larger and broader than in the Kanapoi specimens, but otherwise agreement is good.

FLUVIATILE SERIES (UNIT 3)

Specimen KNM–LT 298 is the front part of an upper LM^3, broken behind the second pair of lateral pillars, but retaining the second median pillar. The lateral pillars are a little more tapered and smoother than in the Kanapoi material and lack the dentate "paramolars" displayed in the other specimens of *N. plicatus*. In this respect they are thus somewhat more like the third molars of *N. pattersoni*, but a great deal larger; the resemblance to *N. plicatus* is otherwise close. The present length is 43.5 mm and cannot have been less than 60–65 mm even if allowance is made only for a modest talon complex; the anterior breadth is 32.9 mm and the height of the unworn anterior pillars is 33.2 mm.

Suidae indet.

Two specimens from Member B of Unit 1 do not seem to belong to *Nyanzachoerus* and are difficult to place.

Specimen KNM–LT 317 is a right upper canine, found with the holotype skull of *Nyanzachoerus tulotos* but it does not fit the alveoli in the skull. It is curved fairly strongly in the horizontal plane and is truncated diagonally by a large wear facet (Pl. 29). The tooth is 12.5 cm long, as preserved, and tapers towards a fairly narrow root. The cross section is almost circular and below the worn facet measured 28.5 mm anteroposteriorly and 27.0 mm dorsoventrally. On the lower surface are the remnants of a band of thick, grooved enamel and there are also remnants of enamel on the upper surface. There is no indication of the inset lateral enamel ridge-bands characteristic of *Potamochoerus.*

Specimen KNM–LT 314 is a left upper third molar, completely unworn but fully formed. It displays the simple basic pattern found in *Sus* or *Potamochoerus.* There are small accessory pillars between the first and second pair of laterals, single on the lingual and multiple on the buccal side. There is a fairly well-developed stout talon pillar. The molar is rather more triangular in outline than that of *Potamochoerus* and more like the form seen in *Sus* and *Nyanzachoerus.* The length is 33.1 mm and the breadth is 22.3 mm anteriorly, 19.2 mm at the second pair of laterals, and 14.5 mm at the talon. The unworn pillars are approximately 14.5–15.0 mm high, but the base of the enamel is damaged and exact measurement is not possible. The pillars are individually rather more separate and distinct than in typical *Sus,* in fact resembling *Nyanzachoerus* more closely in this respect. In the absence of more adequate material it seems best to refer the teeth for the present to an unknown unspecialized suid.

Notochoerus cf. *euilus*

Two specimens from the fluviatile series (Unit 3) seem to belong to *Notochoerus.* One of these, KNM–LT 327, is from the highest horizon and the other, KNM–LT 297, is from the lower part of this series at about the same horizon as the partial LM^3 of *Nyanzachoerus plicatus* (KNM–LT 298) described above. These three specimens are the only Suidae from Unit 3.

KNM–LT 297 is the back half of a LM$_3$. The length as preserved is 42.0 mm and it may originally have been 65–70 mm. The maximum breadth at the base is 23.3 mm and the height is 35 mm and could originally have been as much as 40 mm. In morphology it is very close to other material referred to *Notochoerus euilus,* although the columns are more tapered than is usual.

KNM–LT 327 is a fragment of the right mandibular ramus with a badly damaged M$_2$, the front half of M$_3$, and the posterior root area (Pl. 30). The second molar is very damaged but its length at the base was about 25 mm and the breadth approximately 19 or 20 mm. The length of the front part of the RM$_3$ is 46.0 mm, and it is estimated that the length of the entire tooth was close to 70 mm. The breadth of the crown is 22.8 mm anteriorly and 24.6 mm at the second pair of laterals; this width relationship has been noted characteristically in specimens from the lower Omo beds that have been assigned to *N. euilus.* The height, as preserved, is 12 mm and the crown is in fairly advanced wear. It can be matched closely in both dimensions and enamel pattern with correspondingly worn teeth from Omo.

Specimen from an Unknown Locality

One specimen collected from the Lothagam area consists of two lower teeth (an LM$_2$ and an incomplete LM$_3$) that are very characteristic examples of *Notochoerus euilus* and can be matched closely with material from the lower Omo beds. They are numbered KNM–LT 289. They were found at an old camp site, known as "Robbins' Camp," which was used by the Harvard expedition; there is no means of determining where they came from originally, except that they were probably collected somewhere in the general region. This may be an indication that a patch of Omo beds (or their equivalent) exists in the neighborhood and has escaped attention.

SUID REMAINS FROM EKORA

At Ekora (see Fig. 1) the upper Kanapoi beds are capped by lava and this is overlain by a moderate thickness of sediments, conveniently termed the Ekora beds. Only a very few suid remains have come from this area, and they include a few teeth of *Phacochoerus* that were not *in situ* and may well have been derived from younger deposits. The upper Kanapoi beds yielded a very small number of fragments (KNM–EK 270) and there is only one specimen from the Ekora beds proper (KNM–EK 271).

Nyanzachoerus cf. *pattersoni*

KNM–EK 270 comprises a few pieces from the upper Kanapoi beds. There is a piece of mandible with RP^4 and part of RM^1; two loose incisors, an LI$_2$ and an RI$_3$; and an LM^3 that had not yet erupted but was probably completely formed. Measurements on the cheek teeth are given in Table 57. The structure and morphology of the teeth agree with those of *N. pattersoni*, but the LM^3 is lower crowned and not as "compact" as in the type material. It is therefore not identified with certainty at the specific level.

Nyanzachoerus cf. *plicatus*

KNM–EK 271, the only suid from the Ekora beds, is an LM$_3$, damaged both anteriorly and posteriorly. Despite this fact, it is structurally so like known material of *N. plicatus* that there can be very little doubt about the identification. It is illustrated in Plate 30.

TABLE 57. MEASUREMENTS ON TEETH FROM THE UPPER KANAPOI AT EKORA REFERRED TO *NYANZACHOERUS* CF. *PATTERSONI*
(EK 270)

Tooth		Length	Breadth		Height
RP^4		18.1	25.2		21.0+
RM^1		20.0e	?		10 +
LM^3	unworn	42.7	28.5	anterior	18.5
			16.3	talon	15.0

AGE AND CORRELATION

The Harvard Expedition Localities

In the three areas studied by the Harvard University expeditions, some age relationships could be determined by field evidence. The Kanapoi beds lie directly below a basalt that can be traced through to the Ekora locality, and the Ekora beds lie above the basalt. The basalt was believed to be a lava flow, although the possibility that it might be a sill cannot be totally excluded. Determinations of age showed a scatter from 2.5 to 2.9 million years, with a mean of about 2.7 million years. The faunal evidence is strongly against such a date, and, until further data on the basalt are available, these determinations are not accepted as definitive of the age of the sediments themselves.[1]

The Lothagam locality is isolated and cannot be tied in stratigraphically to the Ekora and Kanapoi areas. The Lothagam sequence is complex, comprising a lower unit of deltaic deposits, a middle unit of lacustrine beds, and an upper unit of fluvial origin. An intrusive basalt occurs at the contact between the deltaic sequence and the lake beds, and its age of 3.71 ±

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[1] Re-determination on fresh specimens gives an age close to 4.0 million years.

0.23 million years provides a minimum age for the entire sedimentary succession (see Fig. 2).

The distribution of the Suidae at these localities has been given in Table 1. Although the fossil pigs appear to provide a useful basis for correlation, consideration must be given to the possibility that the faunal differences between the various deposits could be the result of ecological factors. However, both *Nyanzachoerus plicatus* and *N. pattersoni* are now known to occur at a number of other localities in East Africa, often together, and *N. plicatus* is found at Lothagam, in the upper horizons, as well as at Kanapoi and Ekora. These facts suggest that ecological differences were at most only of secondary significance.

Although a *Nyanzachoerus* that might be *N. pattersoni* does occur in the deltaic beds of Unit 1 at Lothagam, it is rare and most probably represents an early or ancestral form of the typical Kanapoi species. *N. plicatus* has not been found in the lower part of Unit 1 and is very rare in the upper part of that unit. On the other hand, one of the three specimens of suid from the fluvial beds (Unit 3) is *N. plicatus*, and the other two are *Notochoerus* cf. *euilus*, which is common in the lower part of the Omo beds (see below). *Nyanzachoerus tulotos* has not been found at Kanapoi or at Ekora, and it seems likely that it had become extinct by the time those beds were laid down. The "best fit" correlation from the suid material alone would place the fluvial beds (Unit 3) at Lothagam as approximately coeval with the Kanapoi beds, although perhaps slightly younger and possibly as young as the Ekora beds. If the Kanapoi equivalent lay in the upper part of the unfossiliferous lake beds (Unit 2), the suid distribution would be satisfied. Although the total fauna has not yet been worked out, similar general conclusions have been reached from a study of the Proboscidea by Maglio (1970), except that he suggests closer equivalence between the Kanapoi beds and Unit 3 at Lothagam.

Other East African Deposits

The Olduvai succession is already well known and the fauna has been reviewed by Leakey (1965). Several horizons within the sequence have been dated radiometrically. A basalt that was formerly regarded as the base of the deposits has an age of 1.9 million years, but Hay (1967) has designated it as the Basalt Member of Bed I and suggests that the lower sediments to the west of the Fifth Fault might be older than the Basalt Member in the east. However, little is known of the mammalian fauna in the western area. *Nyanzachoerus* has not been reported from Olduvai and the various peculiar Suidae from Bed I are so far not known from other localities. The specimen that Leakey (1965) tentatively referred to *Notochoerus* cf. *euilus* from Bed I is most probably a juvenile of a different form found at Omo. The typical suid *Mesochoerus olduvaiensis* is represented in the upper part of Bed II and possesses elongate and moderately hypsodont third molars; in the lower part of Bed II the molars are a little lower crowned and shorter, and in Bed I there are a few specimens that cannot be separated from the advanced stages of *Mesochoerus limnetes* (= *M. heseloni* Leakey = *Omochoerus heseloni* of Arambourg) from the upper part of the Omo sequence.

The Omo Beds are known, as a result of recent studies, to have a thickness of more than 1700 feet, within which a number of distinctive tuff horizons have been recognized (Arambourg, Chavaillon, and Coppens, 1967; Howell, 1968). A fairly high tuff, originally designated "H," has been dated at 1.81–1.87 million years, which is close to the age of the *nuee ardente* above the basalt at Olduvai (1.70–1.76 m.y.). Tuff "D," near the middle of the Omo succession, has a date of 2.37–2.56 ± 0.12 million years, and the next-to-lowest tuff "B" has been dated provisionally at 3.75

± 0.20 million years. A tentative interpretation of the faunal succession has been given by Arambourg, Chavaillon, and Coppens (1968) and much of the suid material has been studied independently by one of the present authors. *Mesochoerus limnetes* seems to undergo progressive increase in the length of the third molars, as well as in their complexity, and there is reason to suspect that *M. limnetes* and *M. olduvaiensis* may represent a true lineage, the changes being consistent with the radiometric correlations. Below tuff "C" there occurs abundant material referred to the Kaiso species *Notochoerus euilus* (see Cooke and Coryndon, 1970), but above this horizon the typical large suid is *Notochoerus scotti*, the third molars of which become very elongate and hypsodont in the higher levels. *N. euilus* is characteristic of two sites known as "Brown Sands" and "White Sands" (Howell, 1969), which lie well north of the "Type" area (see Fig. 1) but which are regarded as correlatives of a zone between tuffs "B" and "C." Their age is estimated as close to 3 million years. A *Nyanzachoerus* occurs at both these localities but the material is scanty and it is not certain whether it is *N. pattersoni* or *N. kanamensis*. No specimens have been found that could represent *N. plicatus*.

An isolated locality in the northern part of the Omo area was found and worked by Mr. Richard Leakey and his party, and was designated "Yellow Sands" (see Fig. 1). The sediments are capped by a basalt that has been dated, by a single determination, as 4.05 ± 0.20 million years (see Howell, 1968). Both *Nyanzachoerus pattersoni* and *N. plicatus* have beeen identified from this deposit, but no other Suidae were noted in the material recovered. This suggests a close equivalent in age between "Yellow Sands" and the Kanapoi deposit, a view supported by the proboscidean material (Maglio, 1970). The absence of *N. plicatus* at "Brown Sands" and "White Sands" suggests that the Ekora beds are older, and they are regarded here as probably about coeval with tuffs "A" and "B" near the base of the Omo beds in the Type area. Provided that the Omo age determinations are correct—and they are both numerous and consistent—these faunal affinities are very strongly against acceptance of the 2.9 m.y. age of the Kanapoi basalt as indicative of the age of the Kanapoi and Ekora sediments.

Nyanzachoerus has also been found at a number of other localities in East Africa, including the type material from Kanam. The fauna of the Kaiso Formation in Uganda has been discussed at some length by Cooke and Coryndon (1970), who recognized two main mammalian assemblages from horizons near the bottom and near the top of the 2,000-foot thickness of sediments; these were termed respectively the "Earlier Kaiso" and the "Later Kaiso" assemblages. *Nyanzachoerus* inseparable from *N. kanamensis* occurs in the "Later Kaiso," but specimens from the lower horizons may now be recognized as having a closer resemblance to *N. pattersoni* (which was not known at the time the Kaiso study was undertaken). The general faunal affinities suggest broad equivalence of the "Later Kaiso" with the middle part of the Omo sequence and of the "Earlier Kaiso" with the base of the Omo deposits.

Sediments in the vicinity of the Kazinga Channel and in the northeastern corner of Lake Edward have been regarded as belonging to the Kaiso Formation, although the detailed stratigraphic relations have not been worked out. Material recently discovered by Dr. W. W. Krommenhoek in the area (personal communication) includes a few specimens representing both *Nyanzachoerus pattersoni* and *N. plicatus*, thus providing yet another paired occurrence of the two species, as at Kanapoi and "Yellow Sands." A roughly similar age is thus indicated for the particular horizons from which these fossils came.

As far as the age of the Kanam deposit is concerned, some uncertainties exist. The occurrence of *Nyanzachoerus kanamensis* and *Equus* sp. might be taken to imply correlation with the "Later Kaiso." However, Proboscidea of "Earlier Kaiso" and Kanapoi affinities occur at Kanam as well. Preliminary restudy of the material suggests that two different ages may be represented in the Kanam collections, which do not come from a single site. The correlation of the Kanam beds is thus somewhat problematical at the moment.

In the areas west and north of Lake Baringo, systematic mapping by parties from Bedford College (London University) under the direction of Professor B. C. King and Dr. W. W. Bishop has resulted in the discovery of a number of sedimentary formations within a long sequence of lavas and associated rocks. The youngest major group of sediments was named the Chemeron Beds (McCall, Baker, and Walsh, 1967) and was described briefly by Martyn (1967). The sediments are more than 700 feet thick in the centre of the main basin and rest on the Kaparaina Basalts which, in turn, overlie trachytic lavas dated at 5 million years (Bishop, personal communication). A second basin in the same area contains the Kipcherere Beds, which are probably broadly equivalent to the Chemeron Beds. These deposits have yielded only a few mammalian fossils, one of which is a hominid temporal (Tobias, 1967), but the fragmentary remains include two specimens of *Nyanzachoerus pattersoni* and one undetermined fragment that may represent a different *Nyanzachoerus*. The basal parts of the Chemeron and Kipcherere beds, from which these fossils came, thus seem to be broadly equivalent in age to the Kanapoi beds.

Below the Kaparaina Basalts in this region is another sedimentary group known as the Lukeino Beds. These deposits rest on an eroded surface of the Kabarnet Trachytes, which are dated as 7 million years old (Bishop, personal communication). The only suid specimen from the Lukeino Beds is a fragment of skull with much of the palate and most of the cheek teeth. It is clearly a *Nyanzachoerus*, resembling *N. tulotos* in some respects but differing from the Lothagam material in having smaller third and fourth premolars, stronger folding in the main cusps of the molars, and an M^3 that is relatively more enlarged as compared with M^1 and M^2. These characters suggest a form allied to *N. tulotos* but in some respects less specialized and in others modified in a direction towards *N. plicatus*. There are thus apparent resemblances to the Wadi Natrun "*Sivachoerus*" and the Sahabi skull, so that the age may be similar. The Lukeino Beds lie well below another small sedimentary unit called the Kaperyon beds, which do not contain fossil suids but have yielded proboscidean remains which Maglio (1970) equates with the lower beds at Lothagam.

Central and North African Deposits

The occurrence of *Nyanzachoerus* in the Chiwondo Beds of Malawi has already been mentioned (p. 193 above). The specimen is clearly *N. plicatus* and there can be little doubt that the horizon from which it came must be close in age to the Kanapoi beds. This horizon is low down in the Chiwondo Beds, the greater part of which are probably somewhere within the time span of the lower Omo beds. The fauna of the Chiwondo Beds was discussed briefly by Coryndon (1966) and a full account by John Mawby is in the press (personal communication). The giant suid *Notochoerus capensis* is a notable element, together with primitive proboscideans.

In the Lake Chad area, on the southern side of the Sahara, an australopithecine cranium was recovered from one locality in a complex of deposits (Coppens, 1961). A preliminary faunal analysis was made by Coppens (1967) and several stages were recognized for the first time. *Notochoerus capensis* occurs in association with proboscidians resembling those at the base

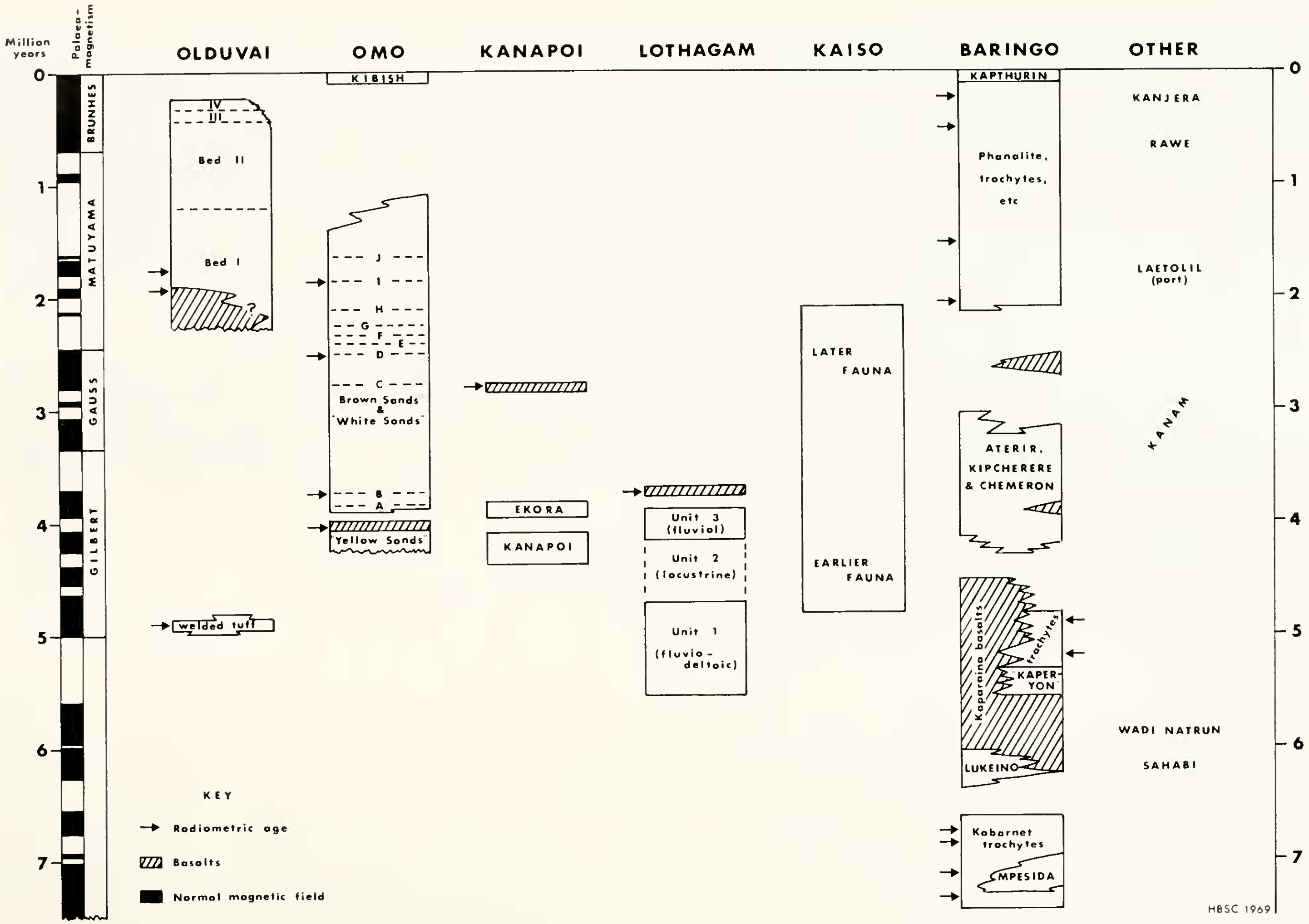

Figure 20. Provisional correlation of Pliocene-Pleistocene deposits in East and North Africa, based primarily on the Suidae. Radiometric dates are shown and are used as controls where possible. The date for the Kanapoi basalt (which lies between the Kanapoi and Ekora sediments) does not accord with the palaeontological evidence and is regarded as anomalous. The sequence for the Baringo area is based on preliminary data supplied by Dr. W. W. Bishop, but the section presented here is a composite one and prepared by the present authors.

of the Omo sequence; a *Nyanzachoerus* has now also been recognized (Coppens, personal communication). As far as can be determined the whole complex ranges over about the span of the Omo beds, but the published data do not allow of more exact correlation of individual sites at the present time.

Until further Sahabi suid material is discovered, and more details are available regarding the whole fauna, the age relations of this site are somewhat uncertain. The lower jaw from Sahabi, *Nyanzachoerus syrticus,* could very well be ancestral to *N. tulotos* from Lothagam, and this suggests a slightly greater antiquity for the North African locality. The skull might represent a form ancestral to *N. plicatus* and there are resemblances to the material from Wadi Natrun and from Lukeino. It therefore seems best for the moment to regard the Sahabi, Wadi Natrun, and Lukeino deposits as roughly equivalent in age and probably a little older than the base of the Lothagam sequence.

The age relations inferred above are set out in tabular form in Figure 20. The conclusions reached are based mainly on the Suidae, and proper correlation must depend on fuller evaluation of the total faunas from each of the sites. It now seems clear that all the deposits that have yielded material assigned to *Nyanzachoerus* are generally older than 3 million years. Although there is not yet agreement on a definition of the base of the Pleistocene, 2.5 million years is a reasonable limit and few authorities have proposed as much as 3 million years. It thus seems reasonable to regard *Nyanzachoerus* as essentially a Pliocene genus. Its earlier Pliocene history is as yet unknown, but new localities are being found and further material is coming to light that may soon clarify existing problems regarding the origin and phylogeny of this genus. Clearly *Nyanzachoerus* is useful for correlation purposes, with a known range from the southern Sahara to Malawi, and it is hoped that the correlations here suggested may assist in the evaluation of relative ages for the important hominid fossils that are being found in increasing numbers in many of these deposits.

ACKNOWLEDGMENTS

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APPENDIX I

NOTES ON *NYANZACHOERUS* SKULL FROM SAHABI

This skull was described by Leonardi (1952) as *Sivachoerus* cf. giganteus Falc.

& Cautl. It was found by Professor Carlo Petrocchi at Sahabi, in Sirtica, north-central Libya and is now in the collections of the Instituto di Geologia e Paleontologia of the Universita degli Studi in Rome; thanks are due to Dr. Carmelo Petronio for making it available for study.

The skull is dorsoventrally crushed and the cranium was apparently lost by erosion before recovery; the dorsal area has been filled with a grey cementlike plaster and further restoration would be difficult. The snout is long and narrow and the nasals are gently arched. The nasals may overhang the maxillae slightly but the curve is smooth and not abrupt as it is in *Potamochoerus.* The nasals are almost parallel sided, with only a limited amount of expansion above the front of the canines. The canine flanges are very small, like those of a female *Potamochoerus* but without any vertical wings. The canines are small and almost circular in cross section, with the anteroposterior dimension at the alveolar border 17.5–18.5 mm and the vertical dimension 14.5–15.0 mm. The tips have been lost since Leonardi photographed the specimen but the illustrations indicate that they were very like those of the female holotype of *Nyanzachoerus pattersoni.* In the middle of the broken surface is a small pulp cavity, like that seen in *N. plicatus*, but the canines are not as flattened as in that species. The palate is wider in front of the canines (78.5 mm) than behind them, reaching a minimum of 59 mm just in front of P^2.

The zygomatic arches begin above P^4 and emerge gently at about 30° to the axis of the skull. They then turn to 40°–45° and curve smoothly back almost parallel to the axis at the widest part. Below the orbits the front of the zygoma is rather plate-like and less hollowed than in *N. tulotos* or *N. pattersoni*; this area is not as flat as is inferred for *N. plicatus.* The whole jugal area is thickened laterally and the inner wall of the zygoma is nearly vertical. The inflated portion is hollow and it is crushed on the right side. The outer border droops almost to the palatal plane, thus descending farther than in *N. tulotos.* On the inner side the root of the zygoma extends back as far as the front part of M^3. The ventral surface is almost horizontal and represents a broad area of muscle attachment.

The premaxilla is long and bluntly pointed, as in *Potamochoerus* and in *Nyanzachoerus pattersoni*, and it lacks the truncated tip seen in *N. tulotos.* All six incisors were present in life, but the left I^3 is now missing. I^1 and I^2 are of normal size and are similar in structure, with a simple inner cingulum ridge that encloses a shallow fossette. I^1 is slightly shorter and stouter than I^2 (18 mm by 12.3 mm as against 20 mm by 12.0 mm). I^3 is separated by a gap of almost 10 mm and is a small tooth (10.7 mm by 6.3 mm) that stands erect and looks rather like a miniature canine; the socket on the left side suggests that this is normal. There is a short diastema to the canine and a longer one to P^2. No sign of P^1 exists on either side.

The cheek teeth are in a very bad state, with the enamel pitted and corroded. P^2 is present on the right side, but broken off at the roots on the left. It is a small, simple tooth with a longitudinal median ridge. P^3 is conical, drawn obliquely backwards and inwards, so that the tip lies two-thirds of the way back and lingual to the mid line. There is a small antero-internal cingulum and a larger postero-internal cingulum, the latter almost constituting a low cusp. The outer enamel appears to have been smooth, but the inner side is furrowed either naturally or as a result of erosion. P^4 had a moderately high crown and the main cone is divided into two near the tip. This bifid cone is separated by a transverse fissure from the protocone so that two islands develop with wear. There seems to have been an anterior cingulum ridge almost three-quarters of the height of the main cone and a similar, but smaller, posterior cingulum.

M^1 has been damaged on the left side. On the right it has the two anterior elements

TABLE 58. MEASUREMENTS ON SKULL OF SAHABI *NYANZACHOERUS*

Vertex length	c450		
Basilar length	c400		
Bizygomatic breadth	245		
Greatest breadth across nasals	45–50		
Frontal breadth	c120		
Palatal length	325e		
Width of palate			
between M^3–M^3	29		
between P^2–P^2	38		
Breadth across maxilla outside M^3–M^3	92		
Breadth of maxillae behind inferior border of canines	c105		
Breadth of premaxillae in front of canines	86		
Distance I^3–P^2	95		
Diastema C–P^2	54		
Length premolar series		left 53.5	right 52.0
Length molar series		106.0	104.5
Length P^2–M^3		159.5	156.5

TABLE 59. MEASUREMENTS OF CHEEK TEETH IN SKULL OF SAHABI *NYANZACHOERUS*

Tooth	Length	Breadth	Height
LP^2	root 13.5	root 8.5	–
LP^3	21.5	20.7	21.0
LP^4	18.2	24.1	18.5+
LM^1	gap 21.0	–	–
LM^2	33.3	24.3	18.5+
LM^3	57.0	34.0	27.0
LP^2–P^4	53.5		
LM^1–M^3	106.0		
RP^2	12.3	8.2	7.0+
RP^3	19.0	19.6	21.0
RP^4	17.6	23.6	17.5+
RM^1	21.2	18.8	c5.0+
RM^2	31.7	–	–
RM^3	54.0e	31.5	28.0
RP^2–P^4	52.0		
RM^1–M^3	104.5		

already united into a single island, with a wavy edge. The posterior islands are damaged but it can be seen that the outer one is roughly bell-shaped and the lingual one is more complex. M^2 is badly weathered on the left side of the skull and the right one is damaged externally. The antero-internal column has an island consisting of a rounded lateral element, separated by a constriction from a flattened median element, and another constriction separates this from an axial element; the whole island looks like a concertinaed bell. The antero-external island has a more normal bell shape. The posterior columns are in early wear but conform to the typical *Nyanzachoerus* form. M^3 is almost unworn but the structure of the columns agrees with that seen in the second molars. The maximum crown height of M^3 is almost 28 mm which is slightly less than its anterior basal breadth. It is smaller than any of the corresponding teeth of *N. plicatus* from Kanapoi but the morphology of the tooth, as well as the wear pattern of the islands in M^2 and M^3 is closer to that species than to the other known forms.

Measurements on the skull are given in Table 58 and on the individual cheek teeth in Table 59.

Although the dorsal surface and the occiput of this skull are damaged, it is clear that the temporal-frontal area was broad, as in all the other skulls assigned to *Nyanzachoerus* and unlike the narrow area in *Sivachoerus*. The back of the palate is about level with the back of M^3, as in other specimens of *Nyanzachoerus*, whereas *Sivachoerus* shows a marked elongation of the back of the palate. There is thus no valid reason to continue to assign the Sahabi skull to the Indian genus and it is here regarded as a species of *Nyanzachoerus*.

As far as skull size is concerned, the Sahabi specimen is comparable with the other known species of *Nyanzachoerus*. Compared with *N. tulotos*, the frontal breadth is smaller and the Sahabi skull lacks the lumpy appearance of the Lothagam holotype; the zygomatic arches are generally similar in form, but they droop more and are not as wide in the Sahabi skull; the third molars are substantially larger and the premolars much less robust than in *N. tulotos*; P^1 is clearly absent in the Sahabi

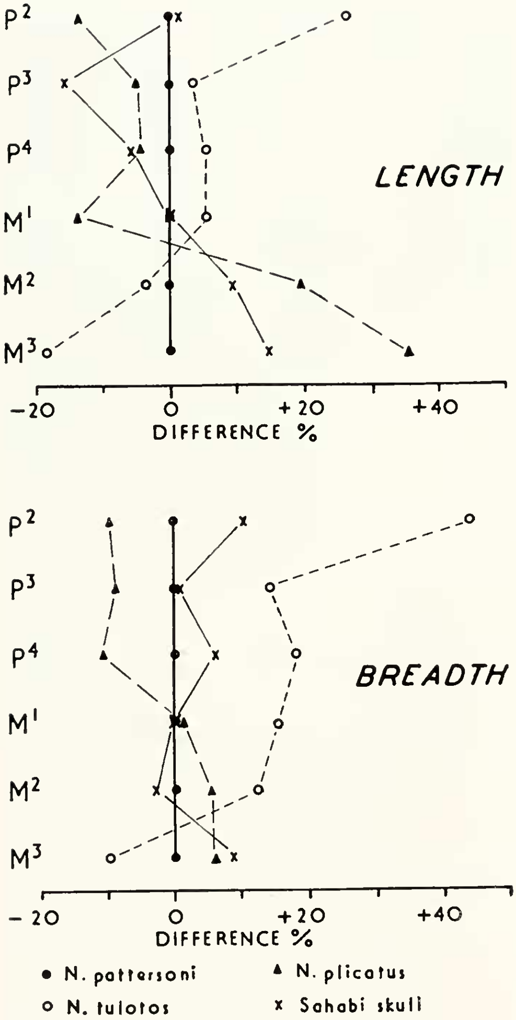

Figure 21. Length (top) and breadth (bottom) of upper cheek teeth in three species of *Nyanzachaerus*, and in the Sahabi skull, expressed as percentage differences relative to the corresponding dimension in *N. pattersoni*. A + shows a larger dimension and a – shows a smaller dimension.

species. Compared with *N. pattersoni*, the morphology of the skull is generally similar, and the canines are of a size comparable to those of the female holotype; the shape of the zygomatic arches is rather different, even from those of the female; the premolars are somewhat smaller and the third molars longer, broader, and with more complex enamel structure; the incisors are more specialized in the Sahabi skull; both species lack P^1.

It is less easy to compare the skull morphology with that of *N. plicatus*, which is known only from fragmentary material, but where the Sahabi skull differs in morphology from the other species, similar points of difference are found in a more advanced stage in *N. plicatus*. Both in *N. plicatus* and in the Sahabi skull the third and fourth premolars are relatively smaller and the second and third molars relatively larger than in *N. pattersoni*. The enamel folding in the second and third molars resembles that in *N. plicatus*, but the complexities are less developed. The canines of the Sahabi skull are intermediate between those of *N. pattersoni* and *N. plicatus*. The unusual incisors cannot be matched, but these teeth are unknown in *N. plicatus*.

Clearly the Sahabi skull must be excluded from close affinity with *N. tulotos*, not only because of the absence of P^1 but also because of important differences in the teeth. In dental characters, as well as in general morphology, it is intermediate between *N. pattersoni* and *N. plicatus*. The premolars are as broad as in the former, but their length is reduced as in the latter. The third molars are both broader and longer than in *N. pattersoni*, but not as enlarged as in *N. plicatus*, and their morphology is closer to the latter. On balance, the Sahabi skull forms a very reasonable ancestor for *N. plicatus* of Kanapoi, having diverged in this direction from an earlier stock which gave rise to the whole *Nyanzachoerus* complex. It is difficult to decide whether the resemblances require it to be placed within the species *plicatus* as an early representative, or whether the differences demand that the Sahabi skull receive a different specific name. The problem would be resolved if the skull of *N. plicatus* were better known. Accordingly it is felt that it is better to leave the matter open at this stage and to designate the Sahabi skull as *Nyanzachoerus* sp. (cf. early *plicatus*).

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Plate 1. *Nyanzachoerus pattersoni* sp. nov. **A, B, C.** Dorsal, right lateral, and palatal views of the holotype (female) skull, KNM-KP 239, from Kanapoi. × ¼.

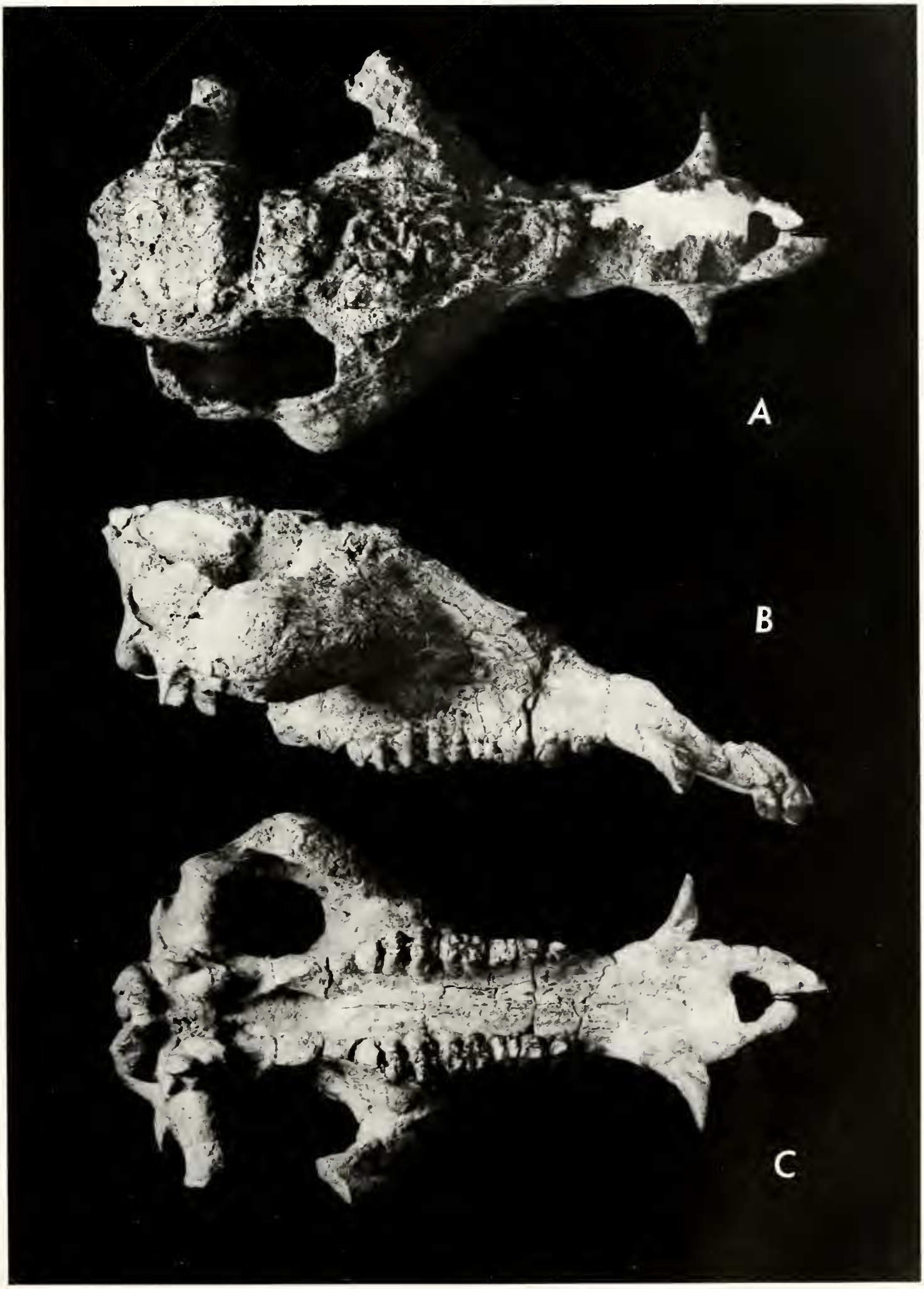
A
B
C

Plate 2. *Nyanzachoerus pattersoni* sp. nov. **A**, **B**. Occlusal and left lateral views of mandible of the holotype, KNM-KP 239. × ¼. **C**. Dorsal view of paratype (male) skull, KNM-KP 264. × ¼.

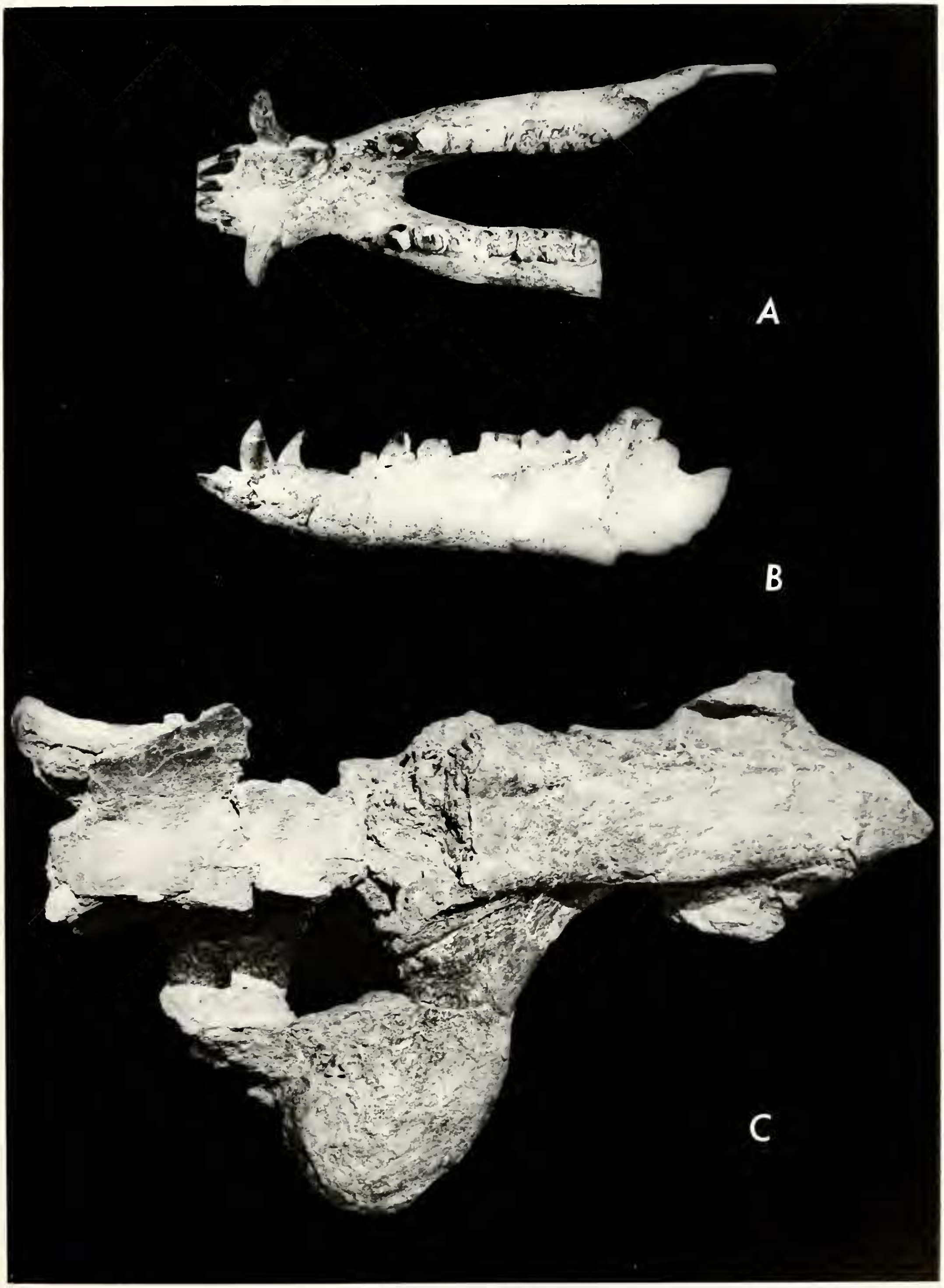
A
B
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Plate 3. *Nyanzachoerus pattersoni* sp. nov. **A**, **B**. Right lateral and palatal views of paratype (male) skull, KNM-KP 264, from Kanapoi. × ¼.

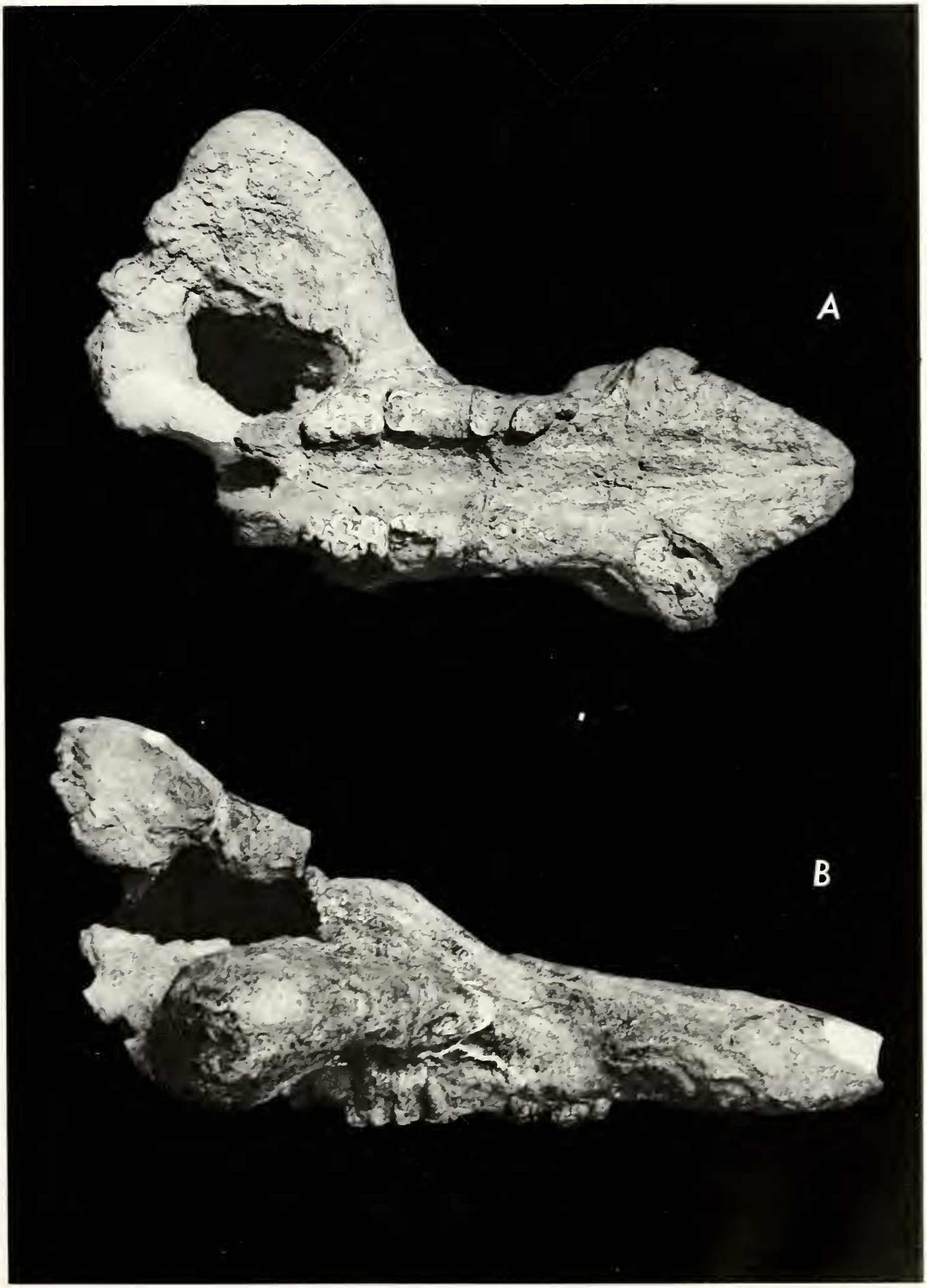
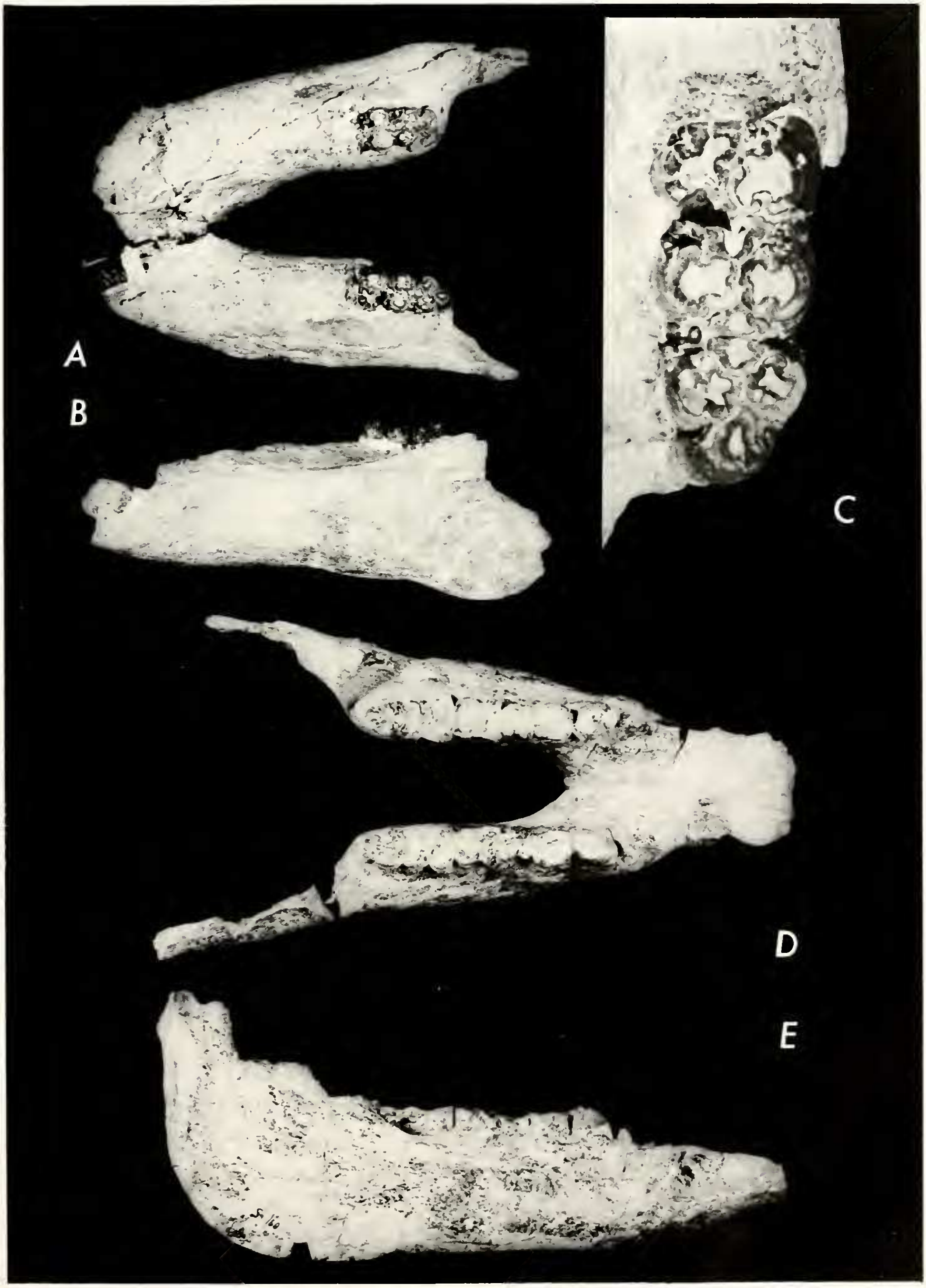

A
B

Plate 4. *Nyanzachoerus pattersoni* sp. nov. **A**, **B**. Occlusal and left lateral views of the massive mandible of the paratype, KNM-KP 264. × ¼. **C**. Crown view of left lower third molar of paratype, KNM-KP 264. Natural size. **D**, **E**. Occlusal and right lateral views of mandible of an old individual, KNM-KP 219, from Kanapoi. (See also Pl. 8). × ¼.


A
B
C
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E

Plate 5. *Nyanzachoerus pattersoni* sp. nov. **A**, **B**. Occlusal and right lateral views of upper cheek teeth in the holotype skull, KNM-KP 239. Natural size.

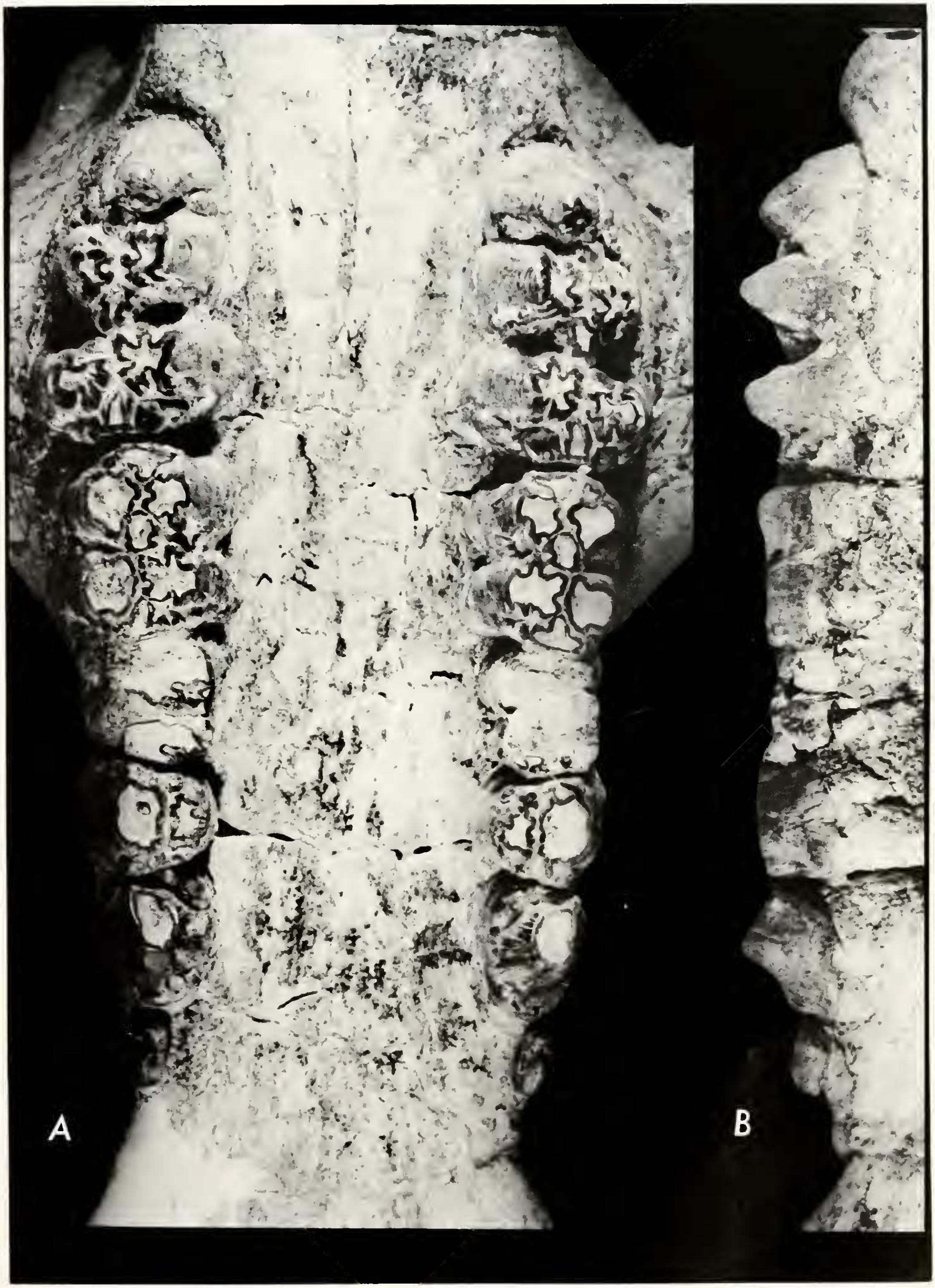

A
B

Plate 6. *Nyanzochaerus pattersoni* sp. nov. **A**, **B**. Occlusal and left outer lateral views of lower cheek teeth in the holotype mandible, KNM-KP 239. Nat. size.

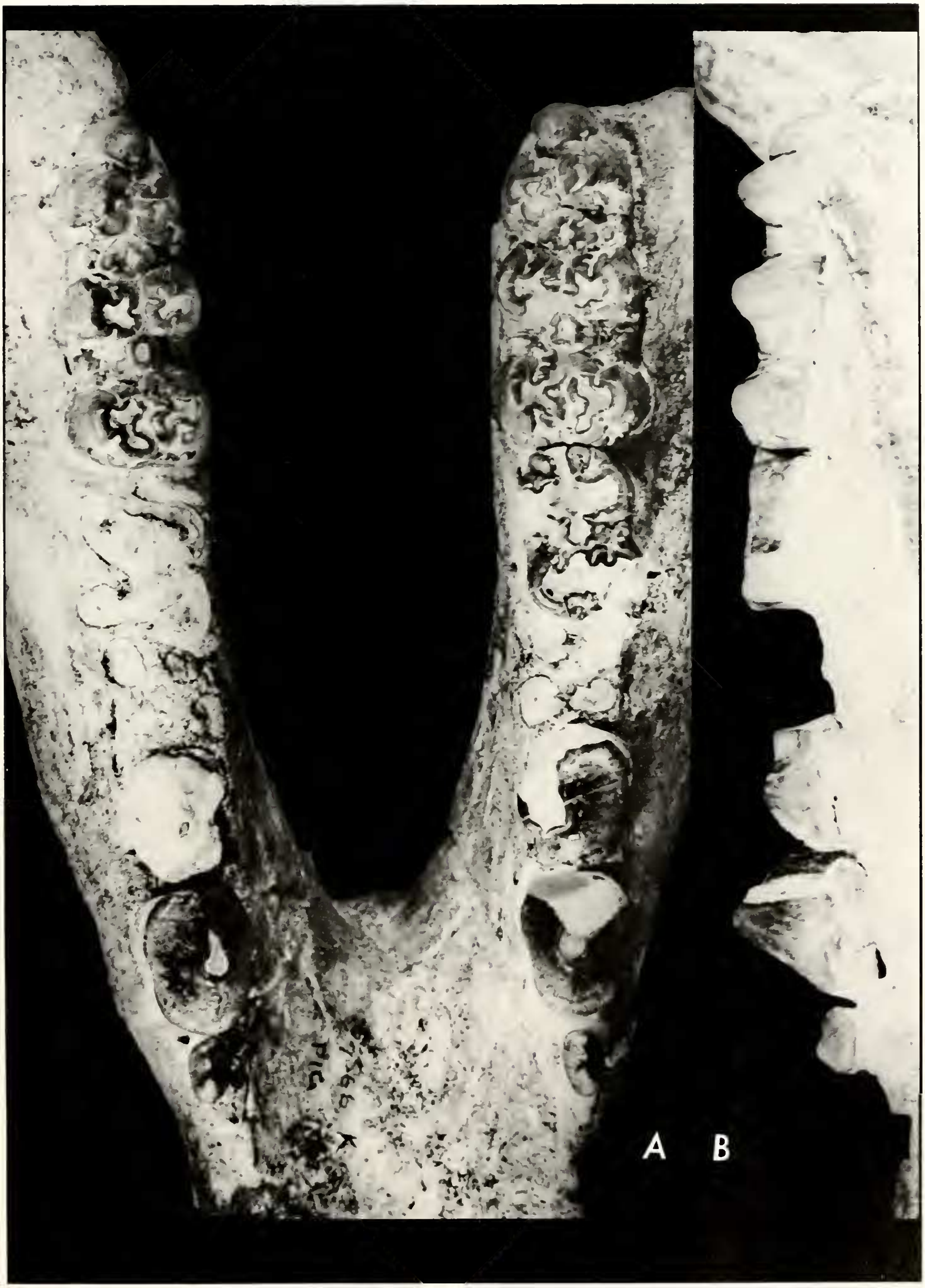

A
B

Plate 7. *Nyanzachoerus pattersoni* sp. nov. Palate and well-worn, damaged cheek teeth in the skull of the paratype, KNM-KP 264. Nat. size.

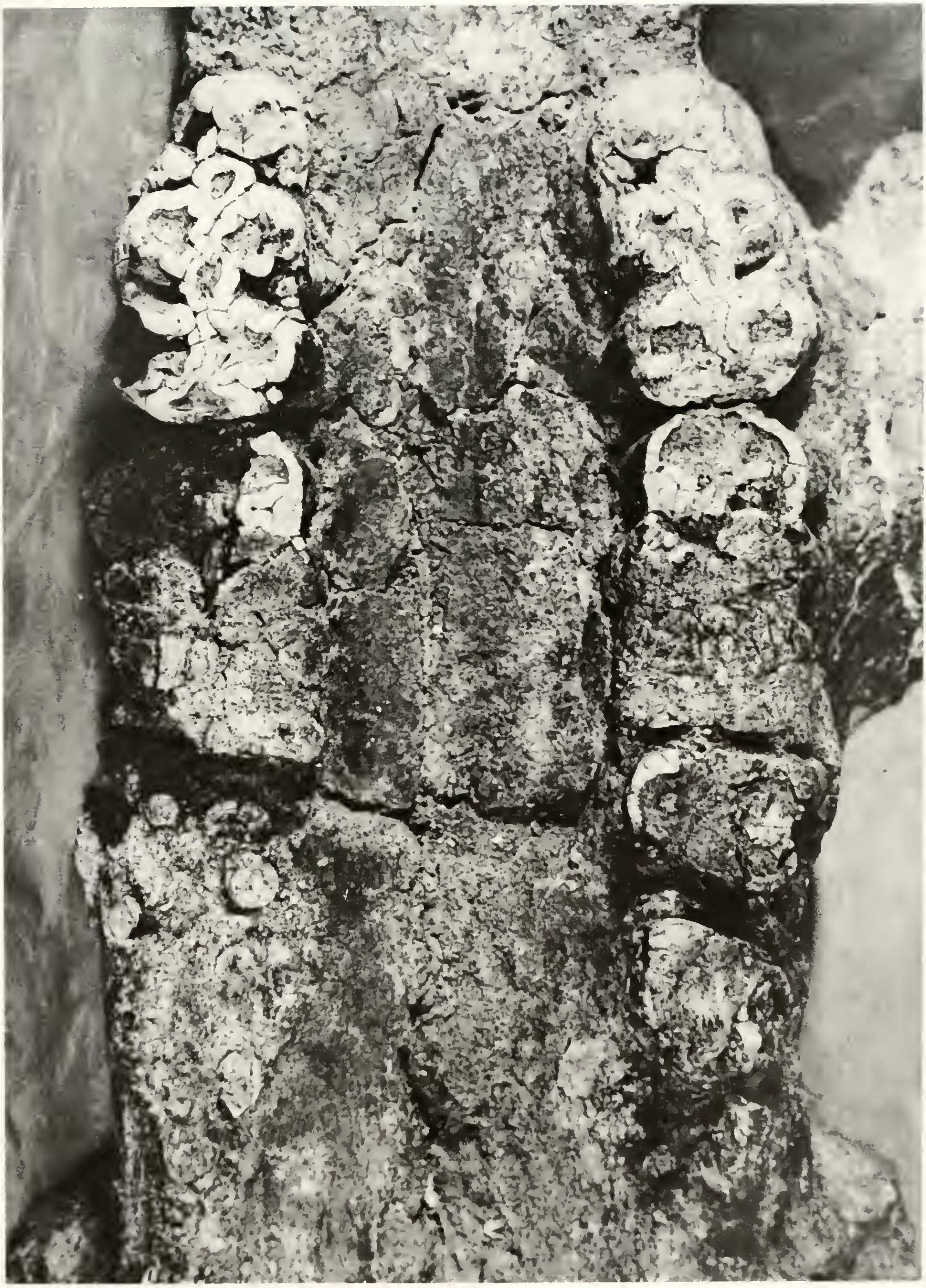


Plate 8. *Nyanzachaerus pattersoni* sp. nov. Occlusal view of well-worn cheek teeth in the mandible of an old individual, KNM-KP 219 (see also Pl. 4). Nat. size.

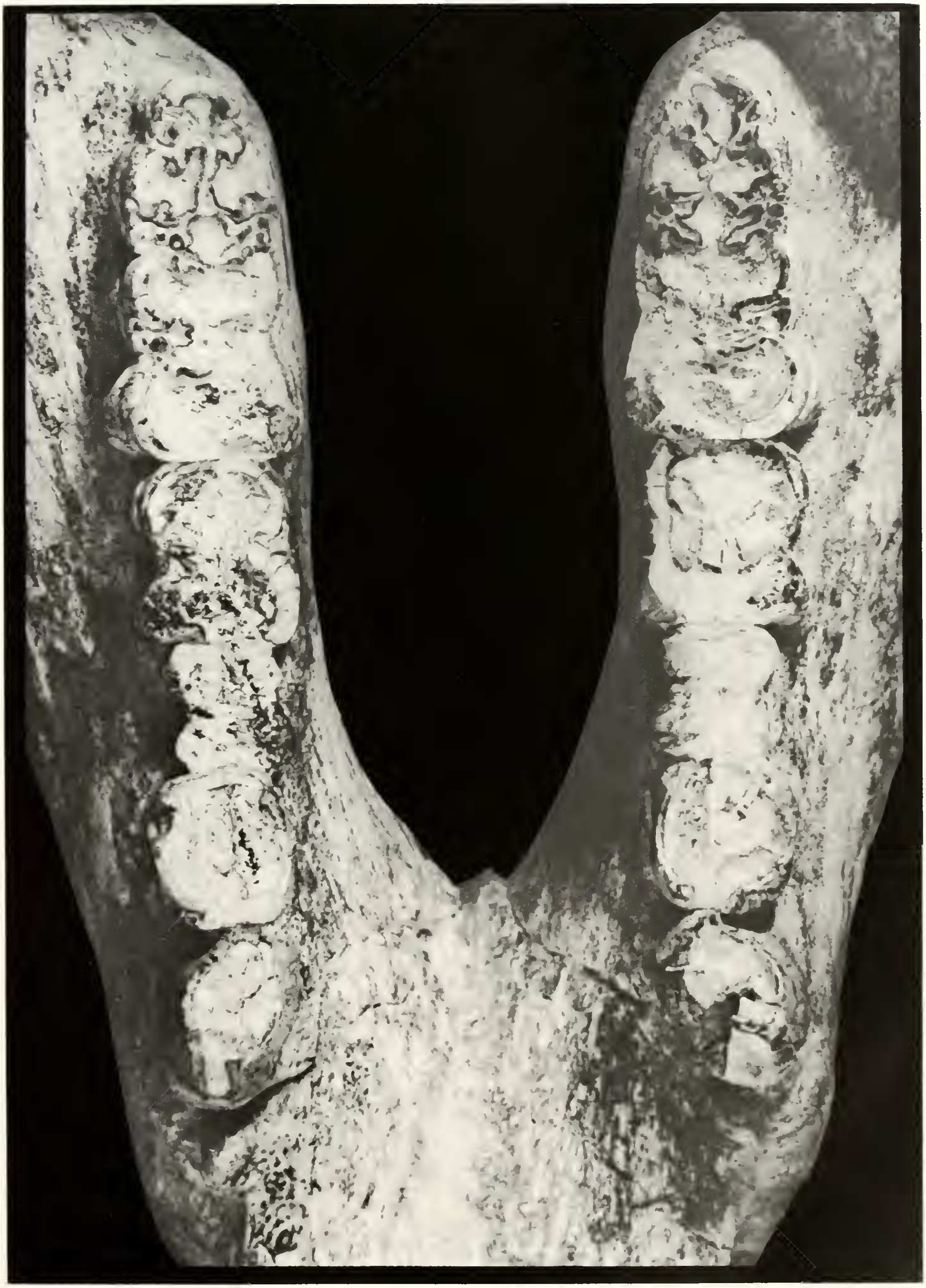


Plate 9. *Nyanzachoerus pattersoni* sp. nov. **A**, **B**. Occlusal and inner lateral views of the left lower cheek teeth in mandibular ramus of a subadult individual, KNM-KP 213. Nat. size. **C**, **D**. Occlusal and inner lateral views of left lower cheek teeth of an adult individual, KNM-KP 263. Nat. size.

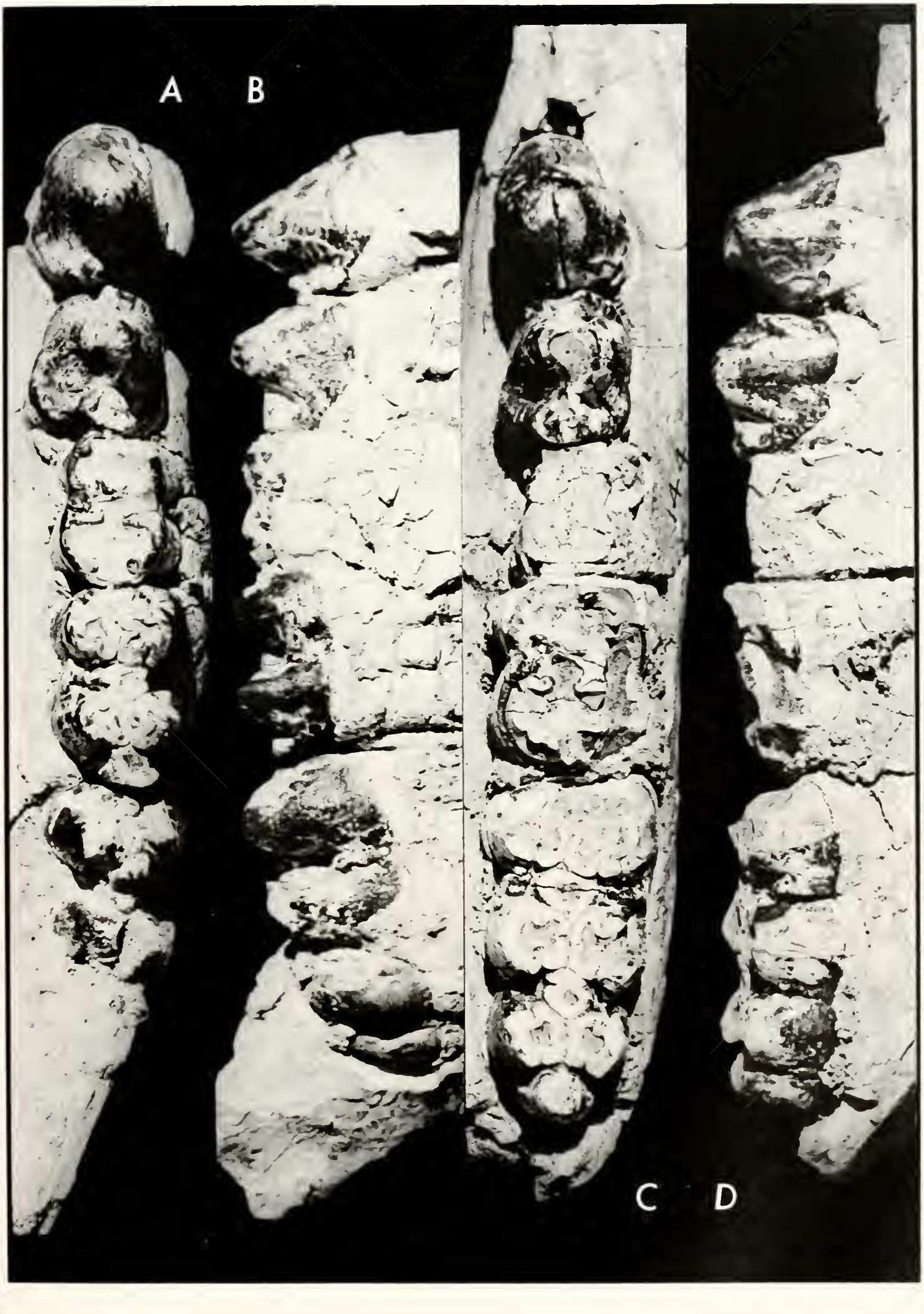

A
B
C
D

Plate 10. *Nyanzachoerus pattersoni* sp. nov. **A**, **B**. Right lateral and palatal views of the skull of an immature (subadult) individual with M^3 unerupted, KNM-KP 244. × ¼. **C**, **D**. Outer right lateral and palatal views of cheek teeth in the immature skull shown in A and B above. Nat. size.

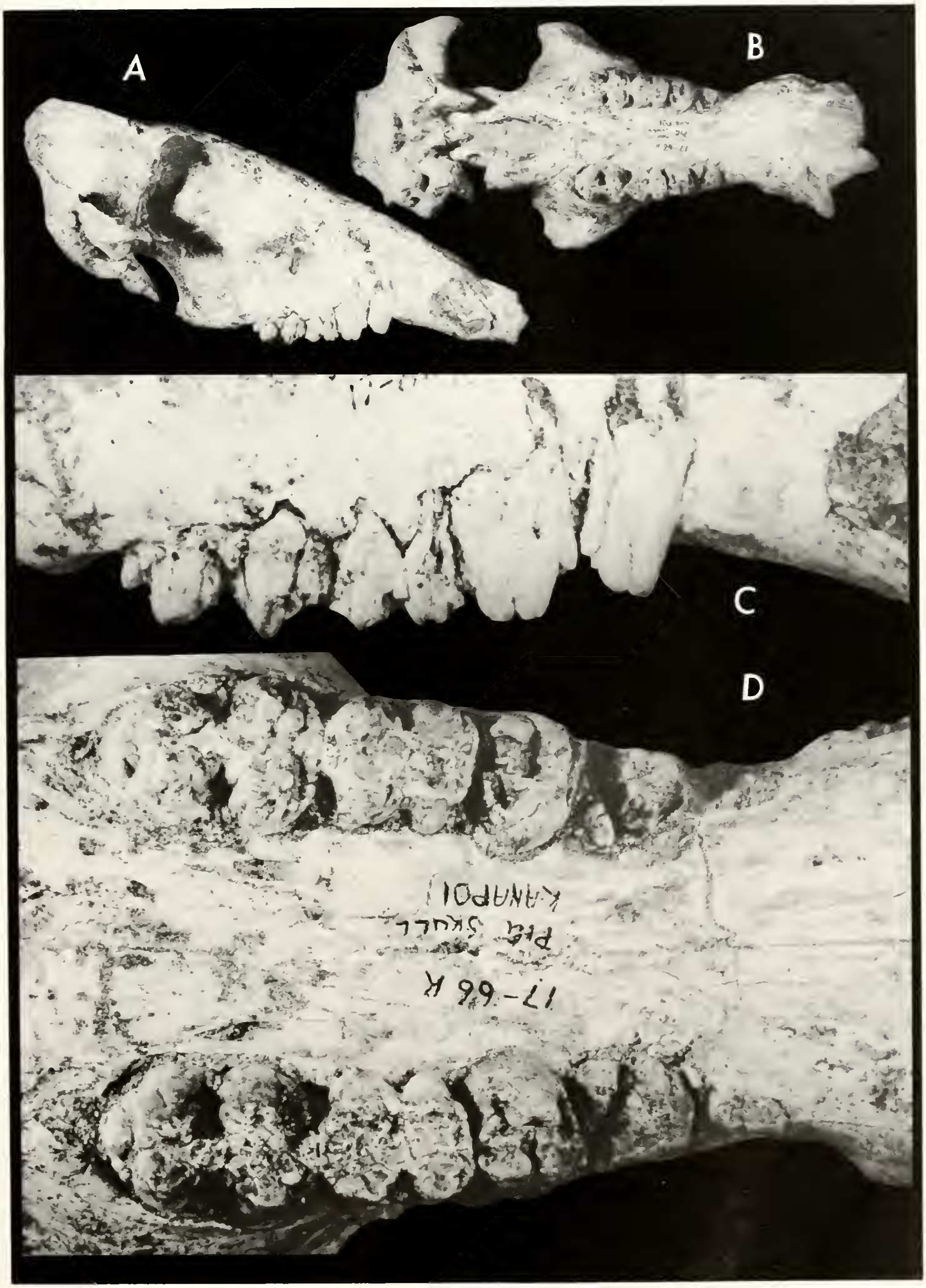

A
B
C
D
17-66 K
PIG SKULL
KANAPOI

Plate 11. *Nyanzachoerus pattersoni* sp. nov. **A**, **B**. Occlusal and inner lateral views of piece of juvenile right mandibular ramus, KNM-KP 221 with dm_{3-4} and M_1. Nat. size. **C**, **D**. Occlusal and inner lateral views of portion of juvenile left mandibular ramus, KNM-KP 221, with dm_{2-4} and M_1. Nat. size. **E**. Dorsal view of symphysis of juvenile mandible, KNM-KP 221 with LdI_{1-2}, RdI_{1-3}. Nat. size. **F**, **G**. Dorsal view of atlas of the holotype (F) compared with the atlas of *Hylochoerus* (G). × ½. **H**, **I**. Anterior view of atlas vertebra of the holotype (I) compared with that of *Hylochoerus* (H). × ½.

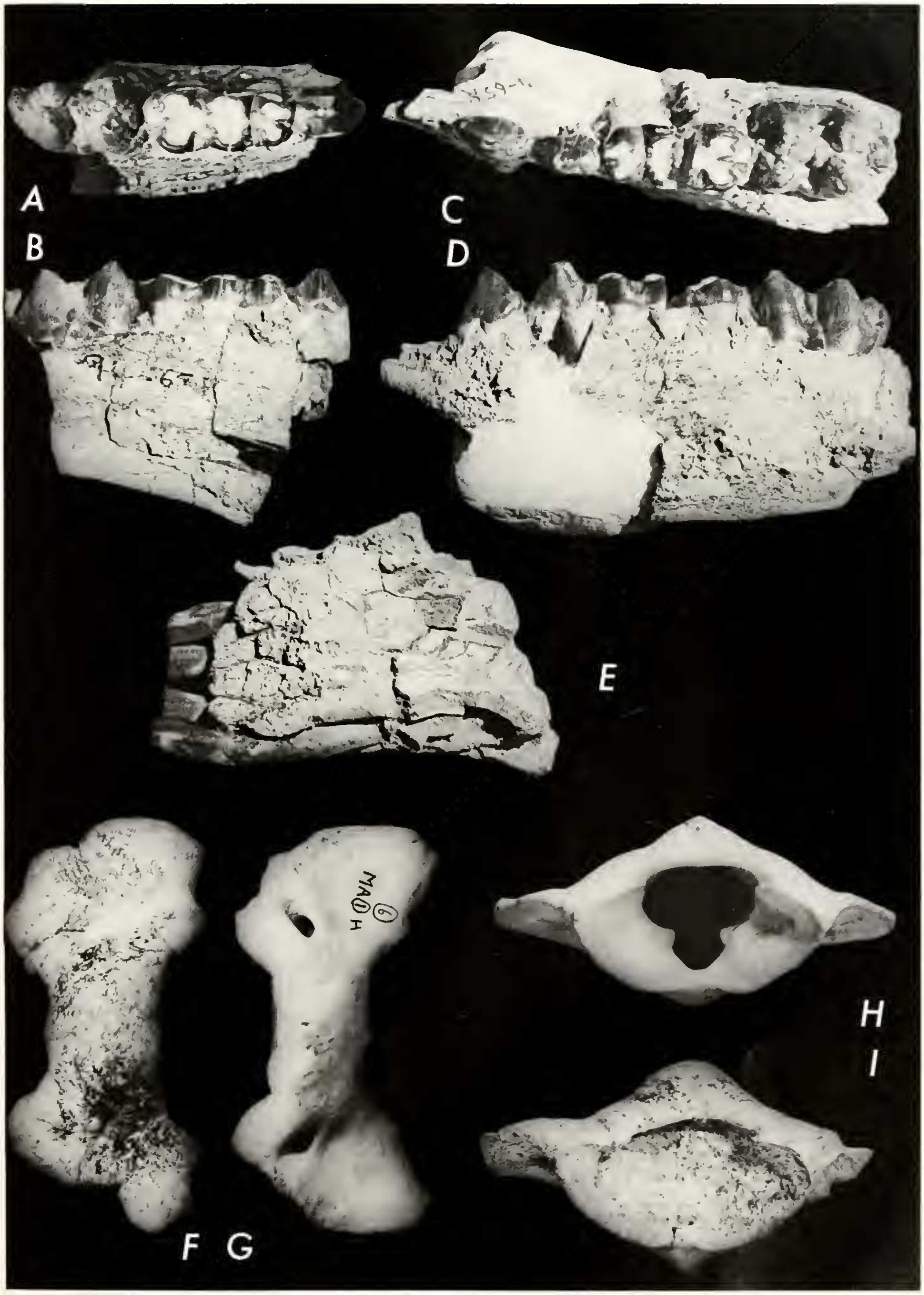

A
B
C
D
E
F
G
H
I

Plate 12. *Nyanzachoerus pattersoni* sp. nov. Associated limb bones, KNM-KP 215. In the centre is the left tibia (A), below which are the matching calcaneum (B), talus (C), cuboid (D), and navicular (E). To the right are bones of the pes; the complete left fourth metatarsal (F) and its matching first phalanx (G), are flanked by the distal end of the metatarsal (H) and proximal phalanx (I), and the distal end of the left fifth metatarsal (J) and its first phalanx (K). L is the first phalanx of the fifth digit of the right side. To the left of the tibia are bones of the right manus. M and N are the first and second phalanges of the third digit. O, P, Q are the three phalanges of the fourth digit; the proximal end of the first phalanx (O) is missing. × ½.

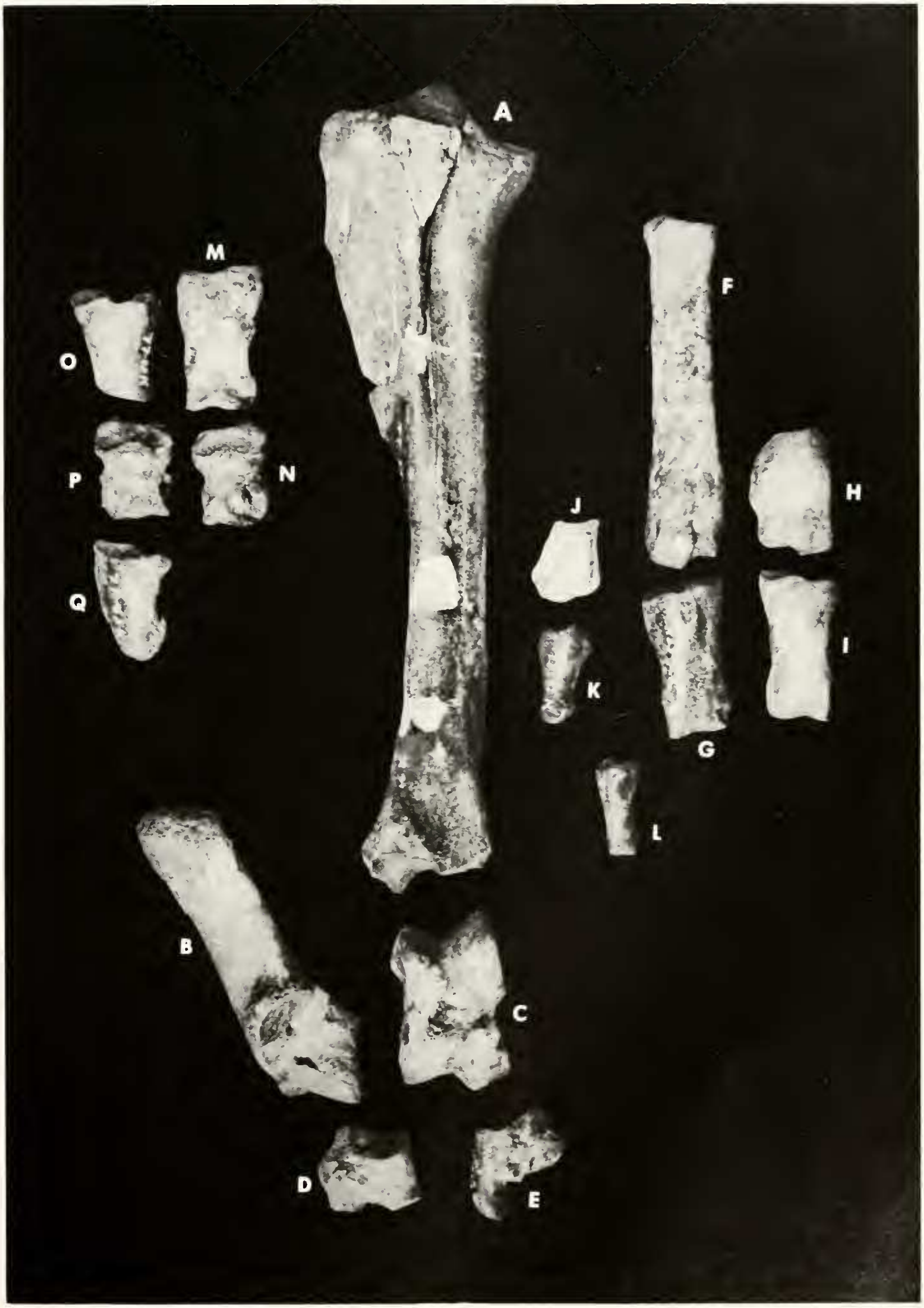

A
M
F
O
P
N
H
J
Q
K
I
G
L
B
C
D
E

Plate 13. *Nyanzachoerus plicatus* sp. nov. **A**, **B**. Dorsal and left lateral views of holotype skull, KNM-KP 251, from Kanapoi. × ¼. **C**, **D**, **E**. Dorsal, palatal and left lateral views of third paratype skull, KNM-KP 257. × ¼.

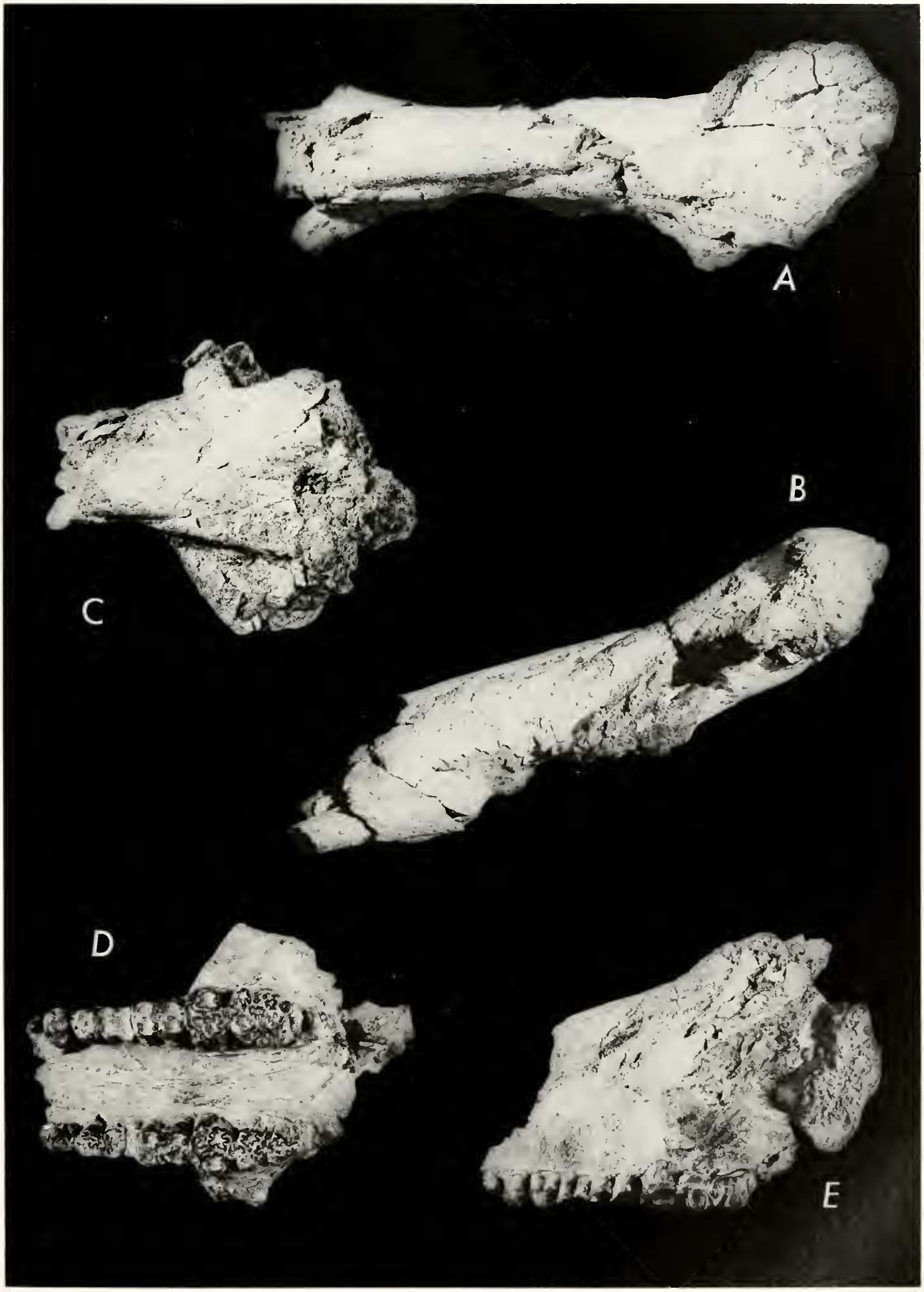

A
B
C
D
E

Plate 14. *Nyanzachoerus plicatus* sp. nov. **A**, **B**. Occlusal and left lateral views of mandible of the holotype, KNM-KP 251. × ¼. **C**. Tip of isolated left upper canine, KNM-KP 203. × ½. **D**. Pair of upper canines and root fragment of a third upper canine, found with the holotype but not belonging to it; cited as first paratypes of the species, KNM-KP 232. × ½.

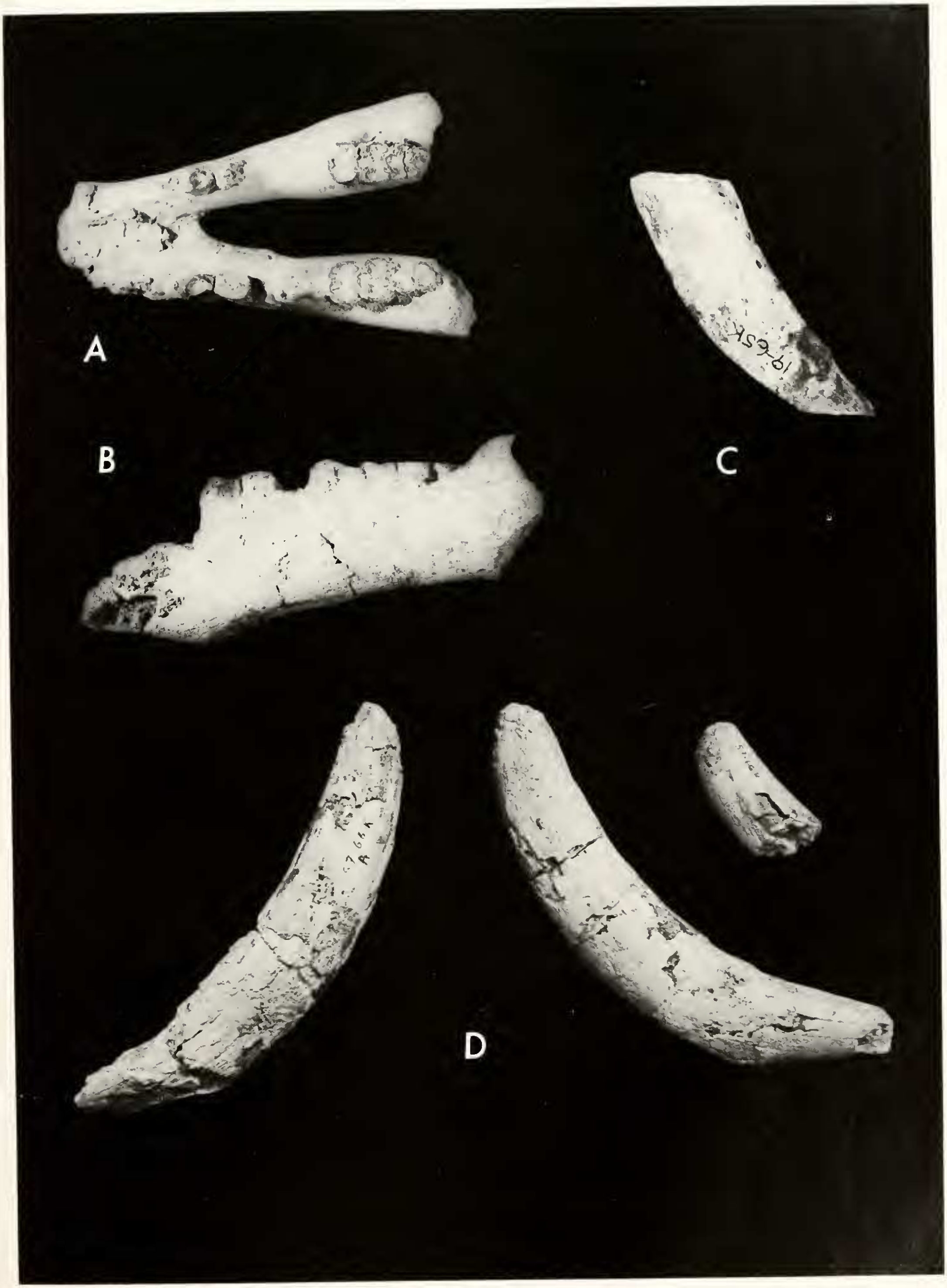

A
B
C
19-65K
D

Plate 15. *Nyanzachoerus plicatus* sp. nov. Associated pieces of second paratype, KNM-KP 262. **A**, **B**. Outer lateral and crown views of upper right second molar. Nat. size. **C**, **D**. Dorsal and ventral views of slightly crushed symphysis with right canine well preserved. × ½. **E**, **F**. Occlusal and inner lateral views of piece of right mandibular ramus with half of M_2 and complete M_3 in early wear. Nat. size.

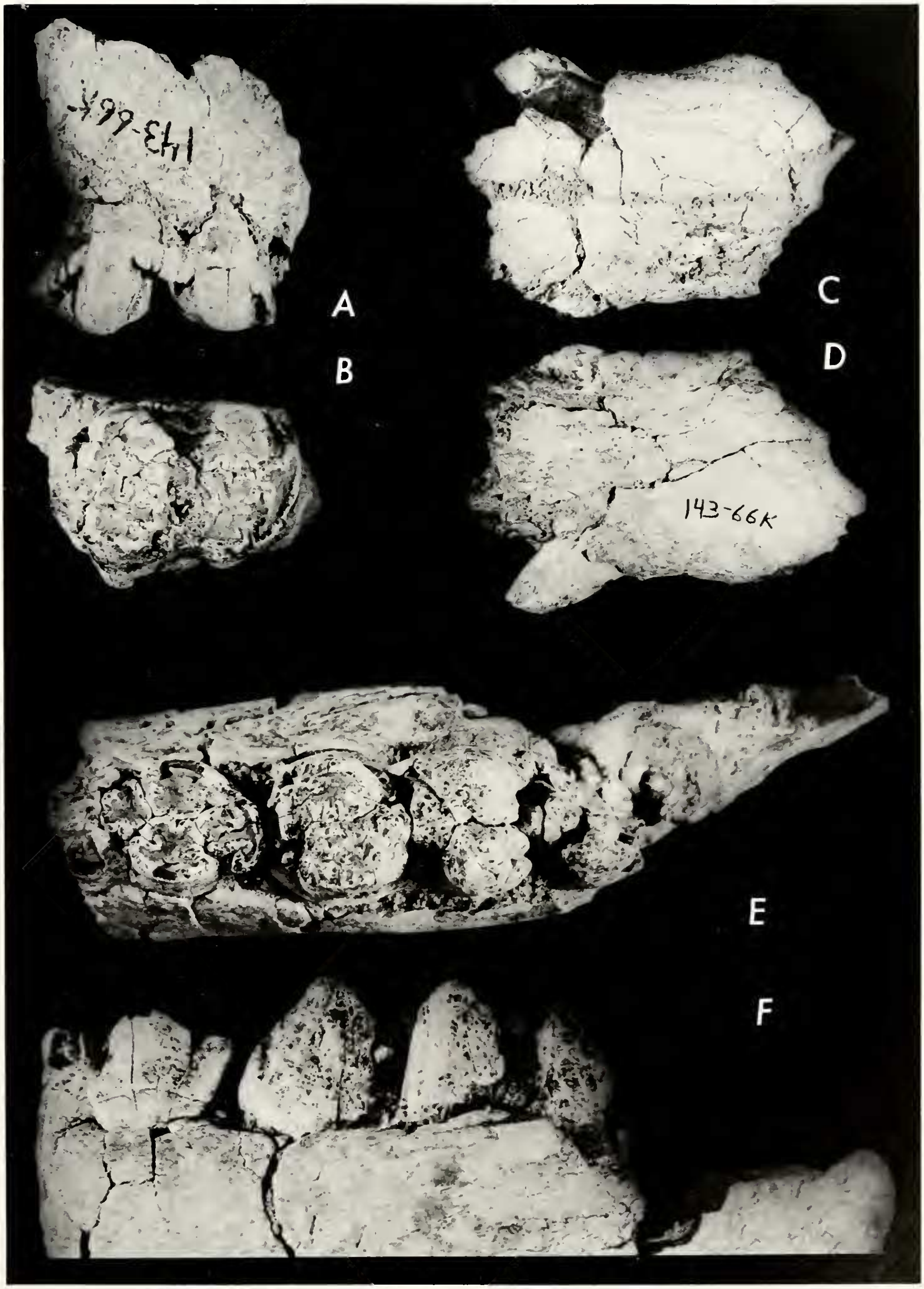

143-66K
A
B
C
D
143-66K
E
F

Plate 16. *Nyanzachoerus plicatus* sp. nov. Palate and cheek teeth of third paratype, KNM-KP 257. Nat. size.

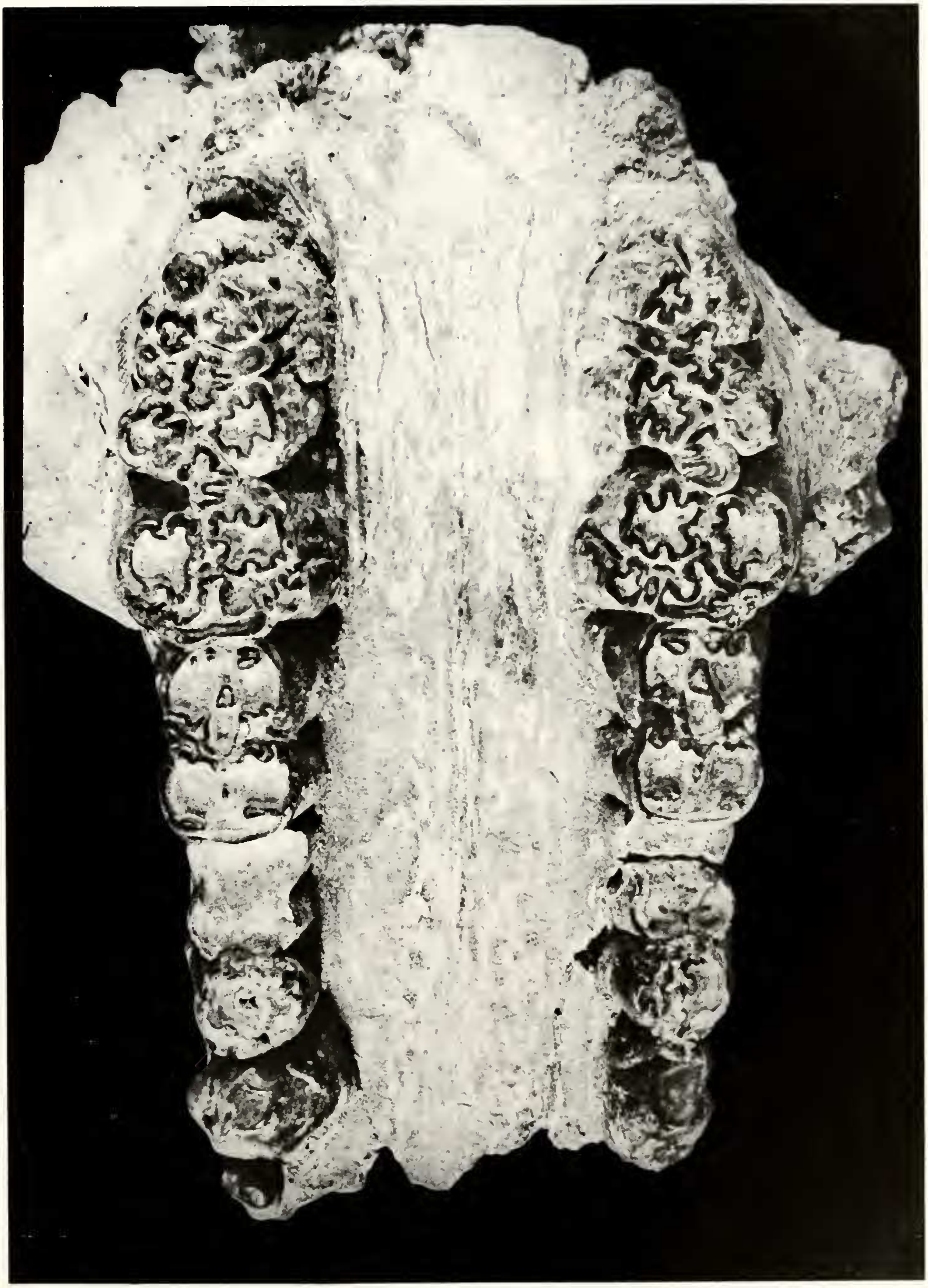


Plate 17. *Nyanzachoerus plicatus* sp. nov. **A**, **B**. Occlusal and inner lateral views of little worn upper right third molar, KNM-KP 225. **C**, **D**. Occlusal and outer lateral views of little worn upper left third molar, KNM-KP 225, found with A, B above. **E**, **F**. Crown view of slightly worn upper left third molar, KNM-KP 235, and view of sectioned surface (F) half way down the height of the crown. **G**, **H**. Crown and inner lateral views of upper right third molar, KNM-KP 253. **I**, **J**. Inner lateral and occlusal views of incomplete unworn lower right third molar, KNM-KP 254. All nat. size.

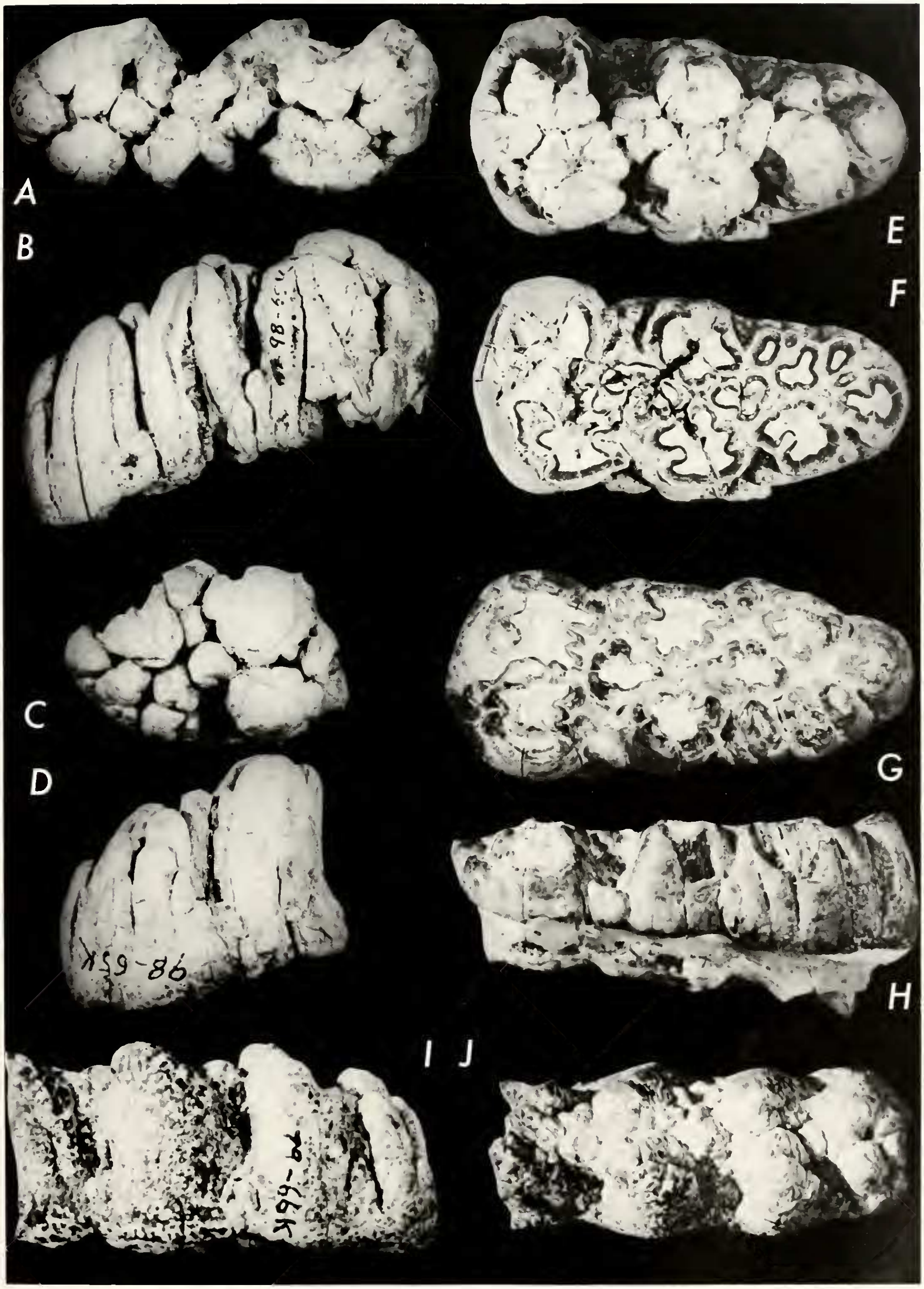

A
B
C
D
98-65K
E
F
G
H
I
J
79-66K

Plate 18. *Nyanzachoerus plicatus* sp. nov. **A**. Crown view of left lower cheek teeth in the mandible of the holotype, KNM-KP 251. **B**. Occlusal view of left mandibular ramus with LM_3 intact and roots of the other cheek teeth, KNM-KP 235. **C**. Occlusal view of fragment of right mandibular ramus of the same individual as B, showing the damaged RP_4, KNM-KP 235. **D**. Outer lateral view of the third molar in B. Note: B–D are associated with the upper molar shown in Plate 17 E, F.

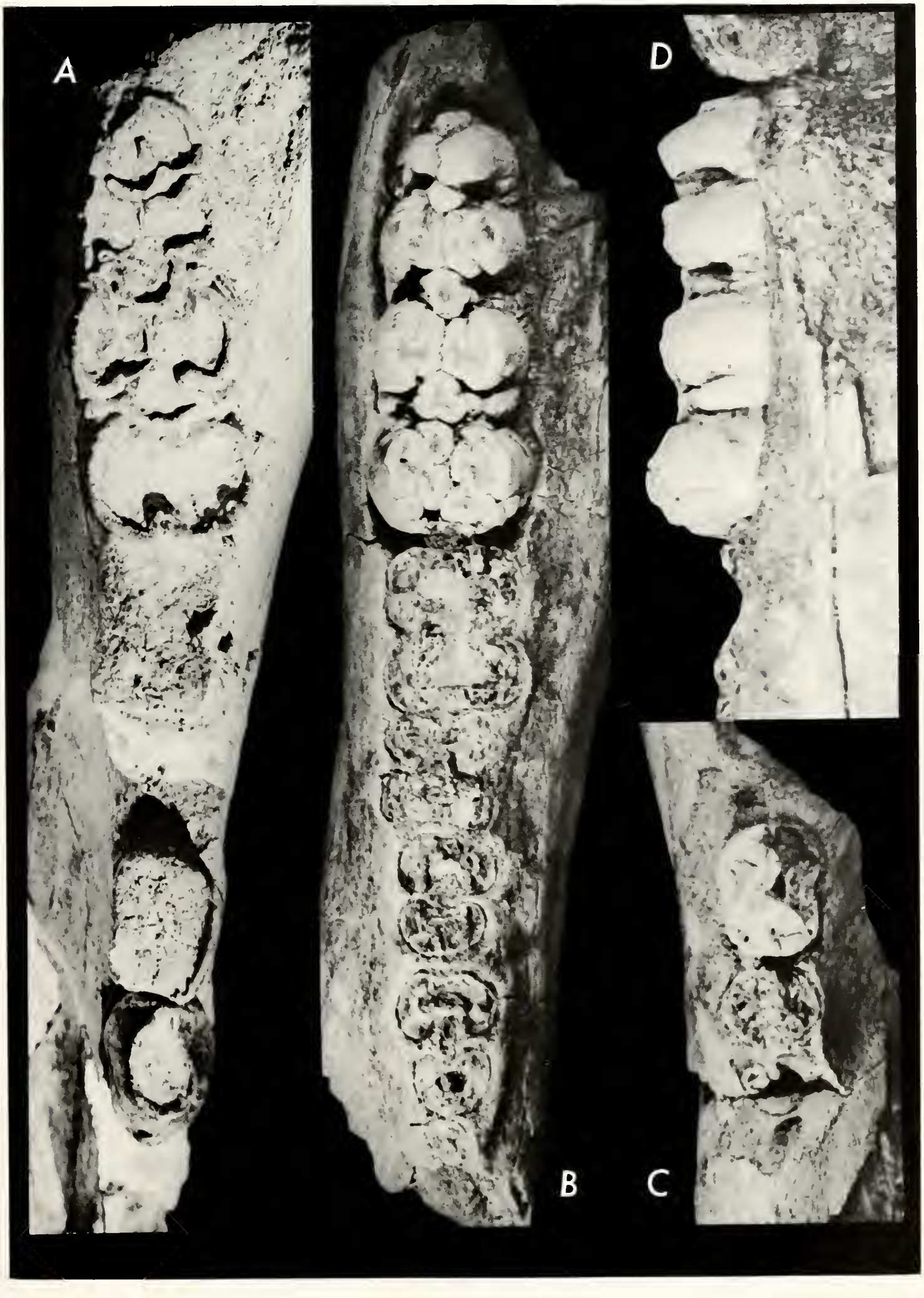

A
B
C
D

Plate 19. *Nyanzachoerus tulotos* sp. nov. **A**, **B**. Dorsal and palatal views of holotype skull, KNM-LT 316, from Lothagam, regarded as male. × ¼.

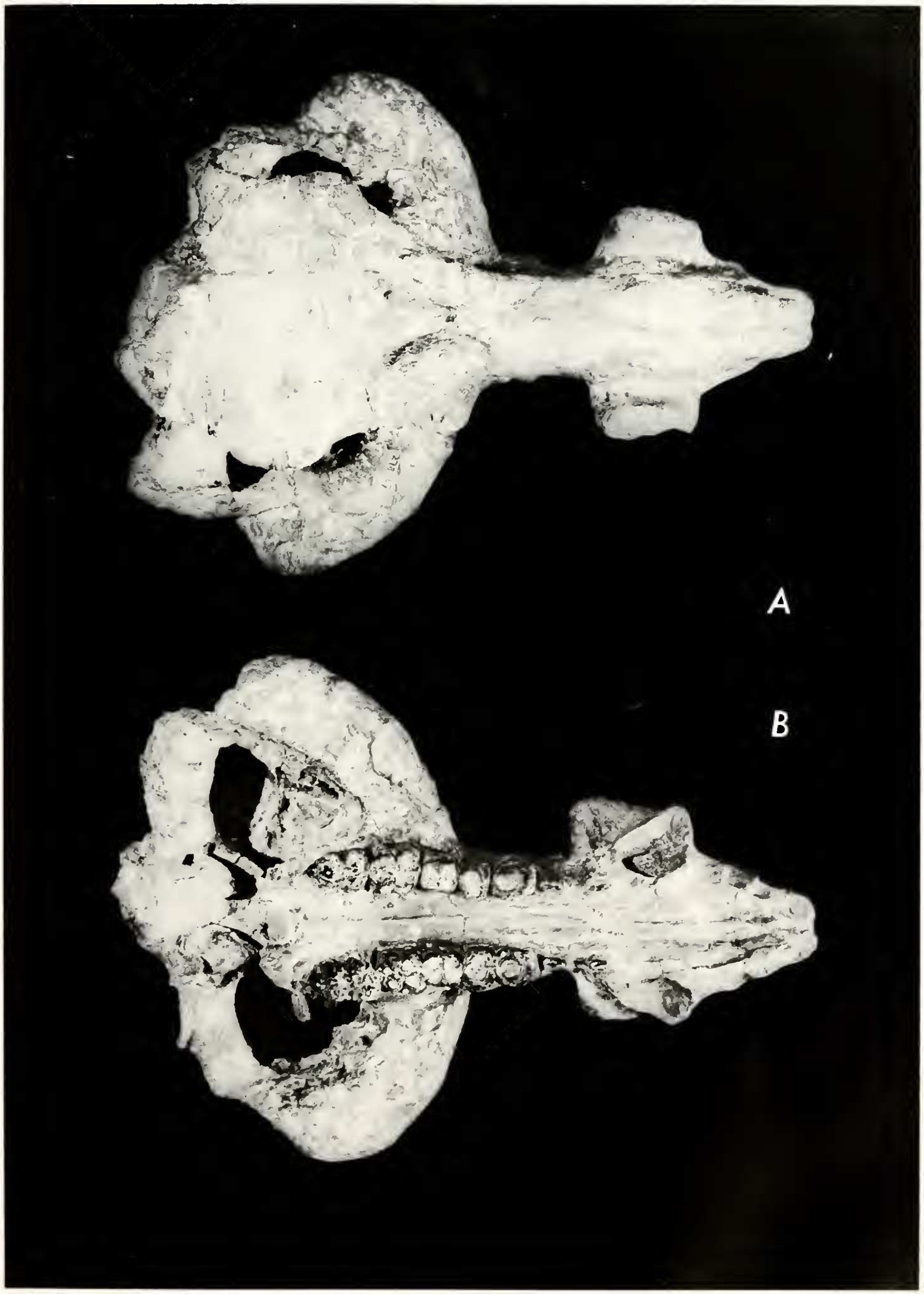

A
B

Plate 20. *Nyanzachoerus tulotos* sp. nov. **A**. Left lateral view of holotype skull, KNM-LT 316. **B**. Occlusal view of incomplete mandible of first paratype, LT 302, regarded as male. **C**, **D**. Occlusal and right lateral views of damaged mandible of second paratype, LT 287, regarded as male. **E**, **F**. Occlusal and left lateral views of mandible of third paratype, LT 295, regarded as female. All ¼ nat. size.

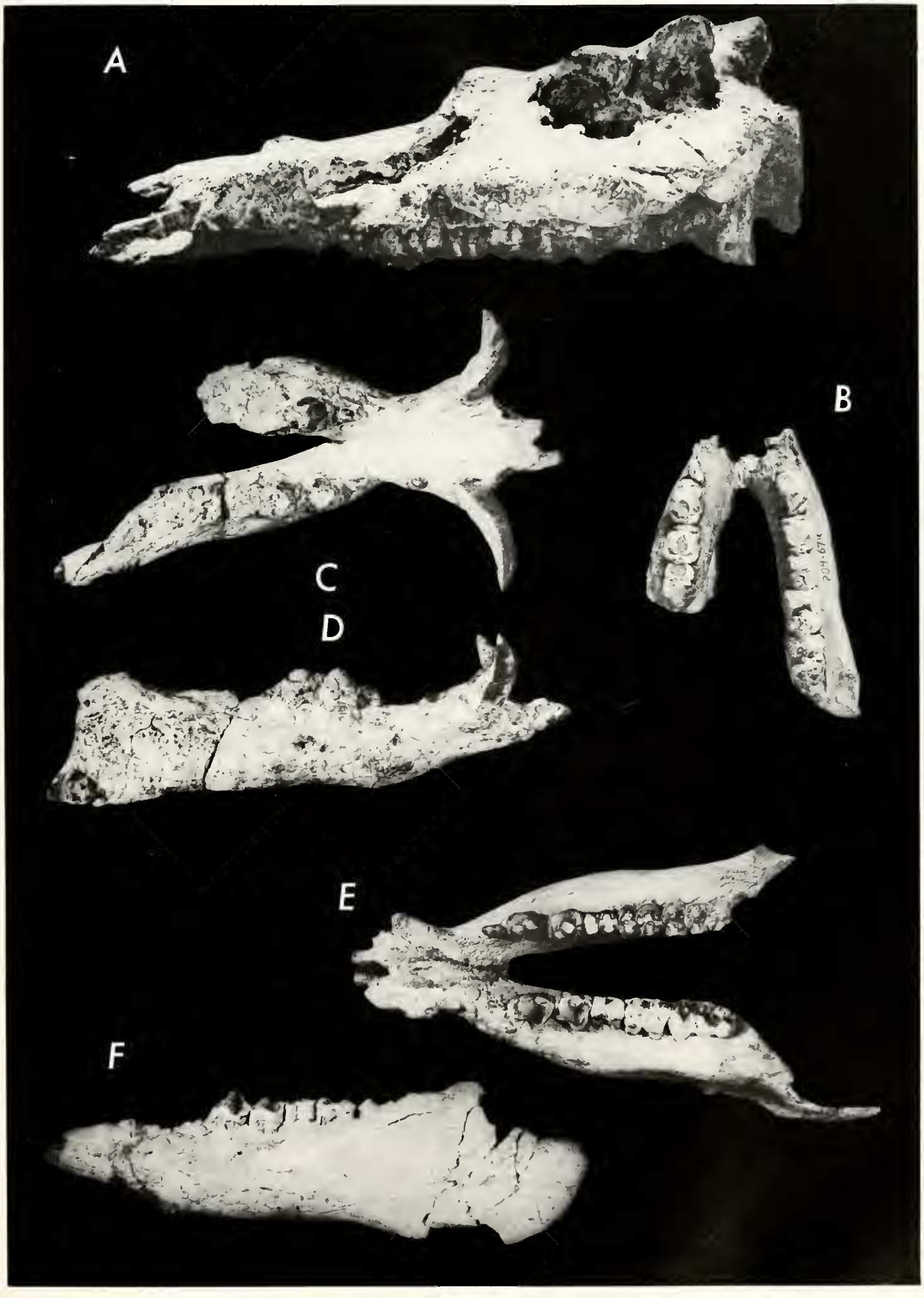

A
B
204-67
C
D
E
F

Plate 21. *Nyanzachoerus tulotos* sp. nov. Palate and cheek teeth of holotype (KNM-LT 316). Nat. size.

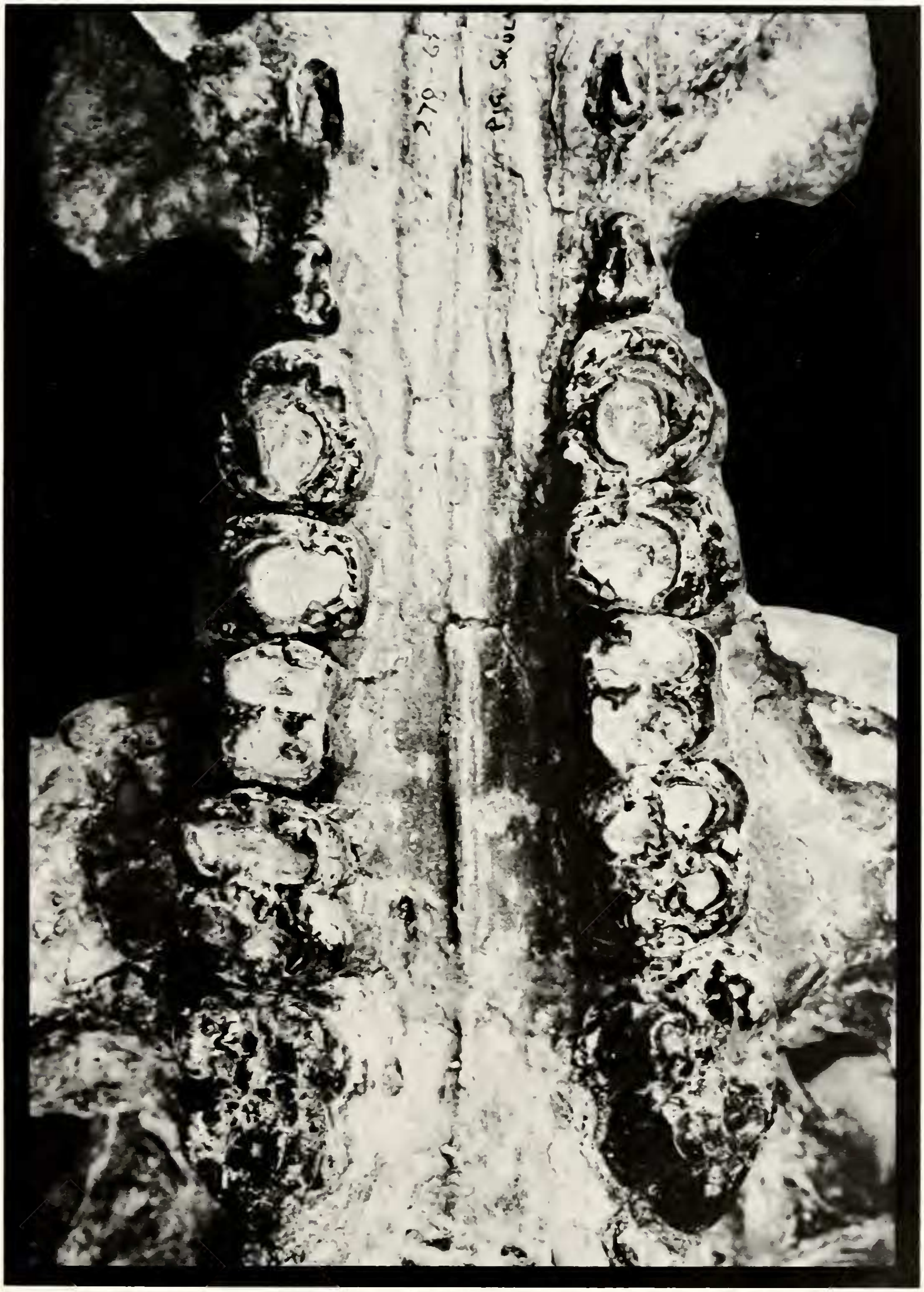

279-67
PIG SKUL

Plate 22. *Nyanzachaerus tulotos* sp. nov. **A**. Occlusal view of lower cheek in the mandible of the first paratype, KNM-LT 302. **B**. Outer lateral view of left lower cheek teeth in A. **C**. Inner lateral view of right lower cheek teeth in A. All nat. size.

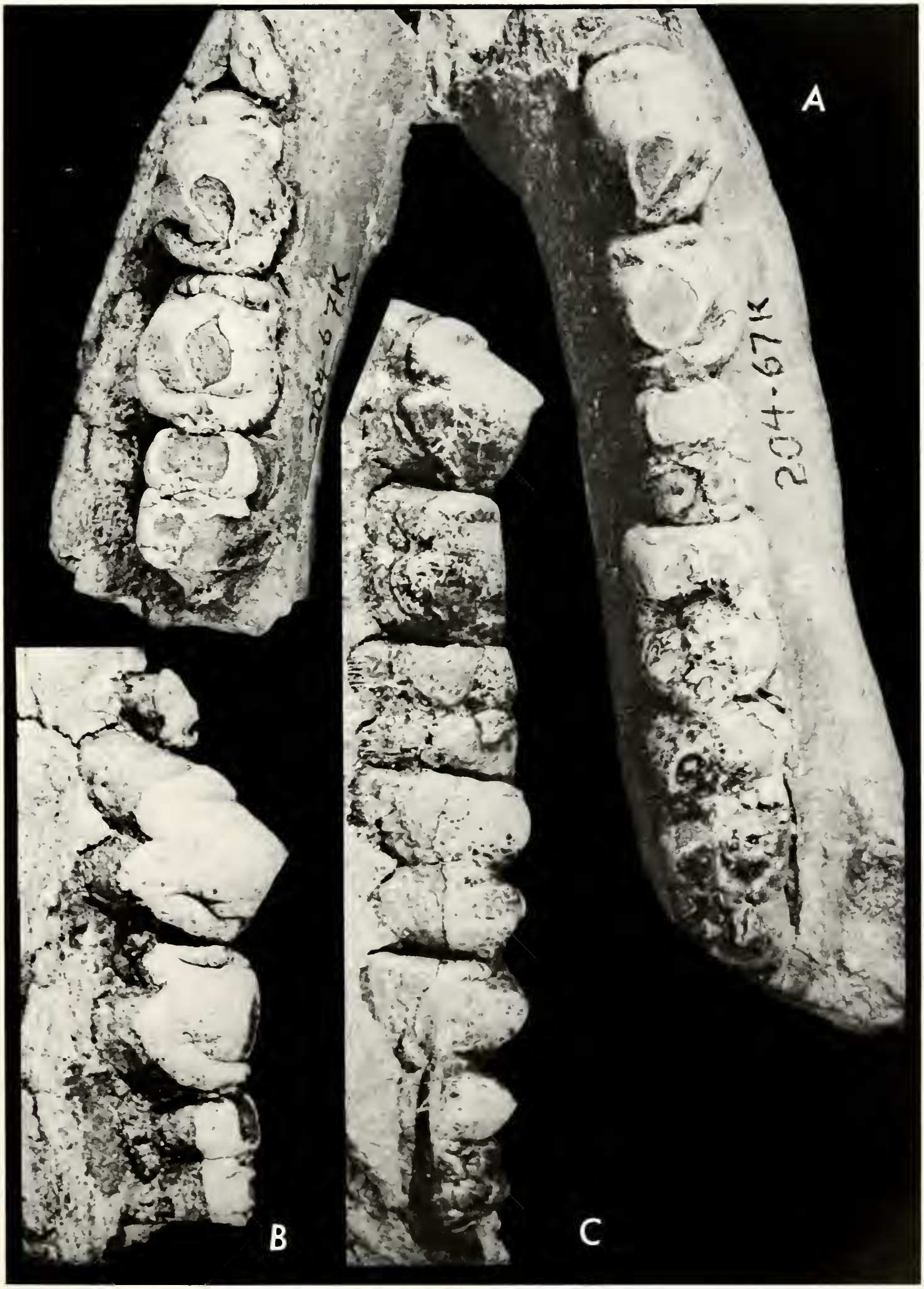

A
204-67K
204-67K
B
C

Plate 23. *Nyanzochoerus tulotos* sp. nav. Occlusal view of lower cheek teeth in mandible of the third poratype, KNM-LT 295. Nat. size.

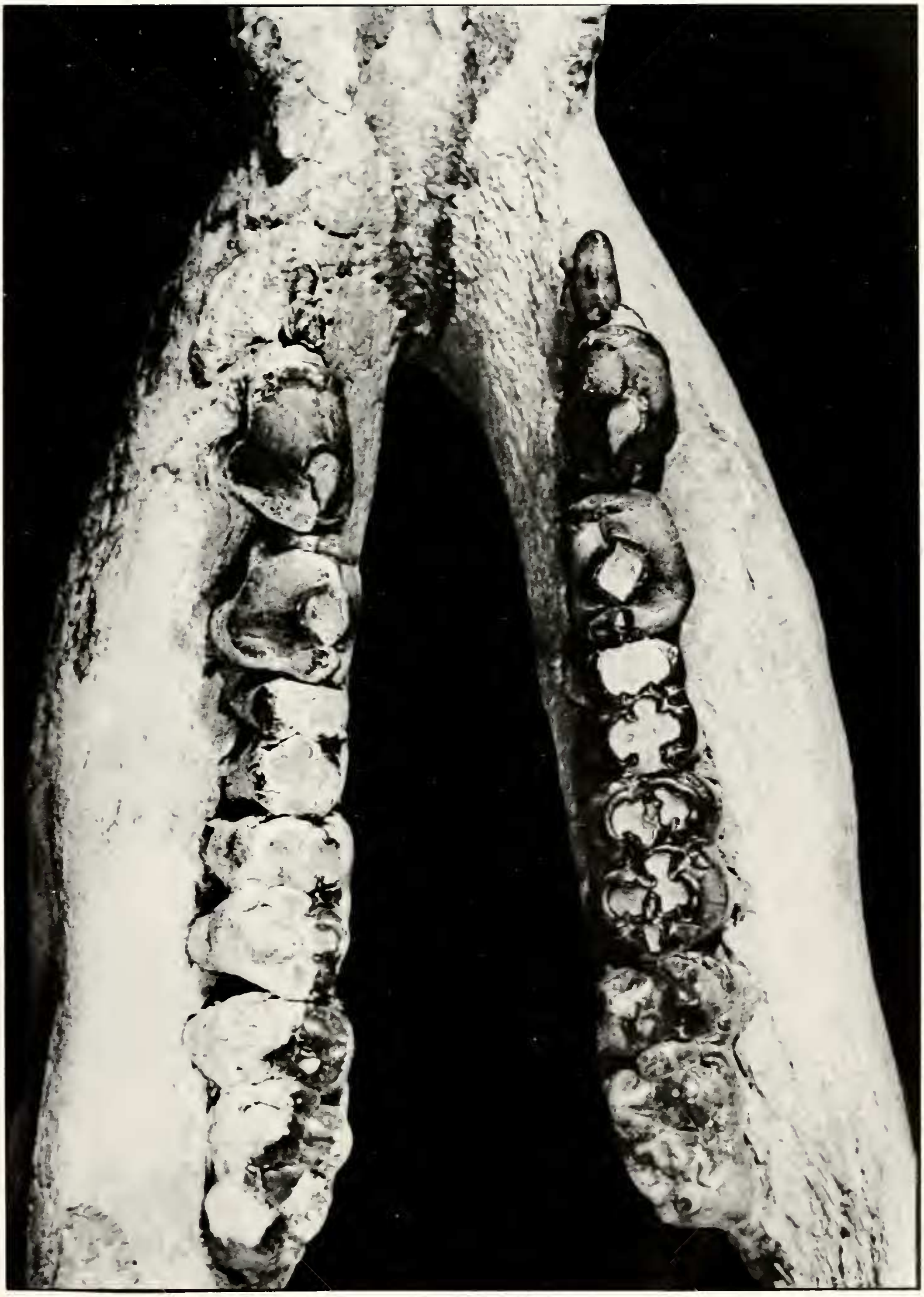


Plate 24. *Nyanzachoerus tulotos* sp. nov. **A**, **B**. Occlusal and outer lateral views of right maxillary fragment with upper cheek teeth of large individual, KNM-LT 313, from Member C of Unit 1 at Lothagam. **C**, **D**. Occlusal and inner lateral views of piece of right mandibular ramus with RM$_3$ and roots of RM$_2$ (KNM-LT 309). All nat. size.

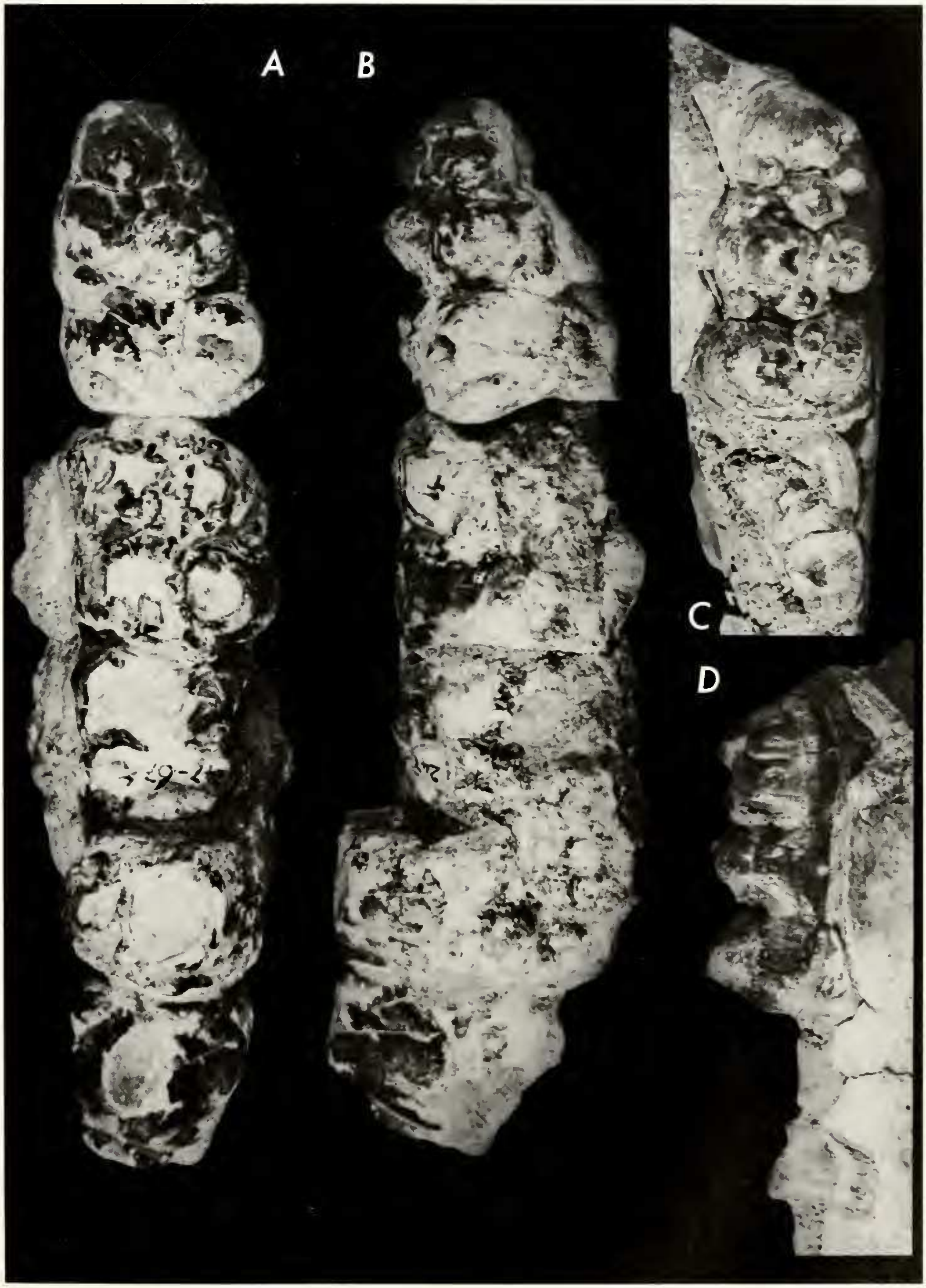

A
B
C
D

Plate 25. *Nyanzachaerus tulotos* sp. nov. **A**. Incomplete, unworn LM^3 and LM^2 (KNM-LT 326) from an uncertain horizon within Unit I at Lothagam. **B**, **C**. Crown and outer lateral views of RM^3 in fragment of maxilla (KNM-LT 324) from Member C of Unit 1 at Lothagam. **D**, **E**. Crown and inner lateral views of unworn RM^3 (KNM-LT 321) from Member B of Unit 1 at Lothagam. **F**, **G**. Crown and inner lateral view of little worn RM^3 (KNM-LT 286), from Member C of Unit 1 at Lothagam.

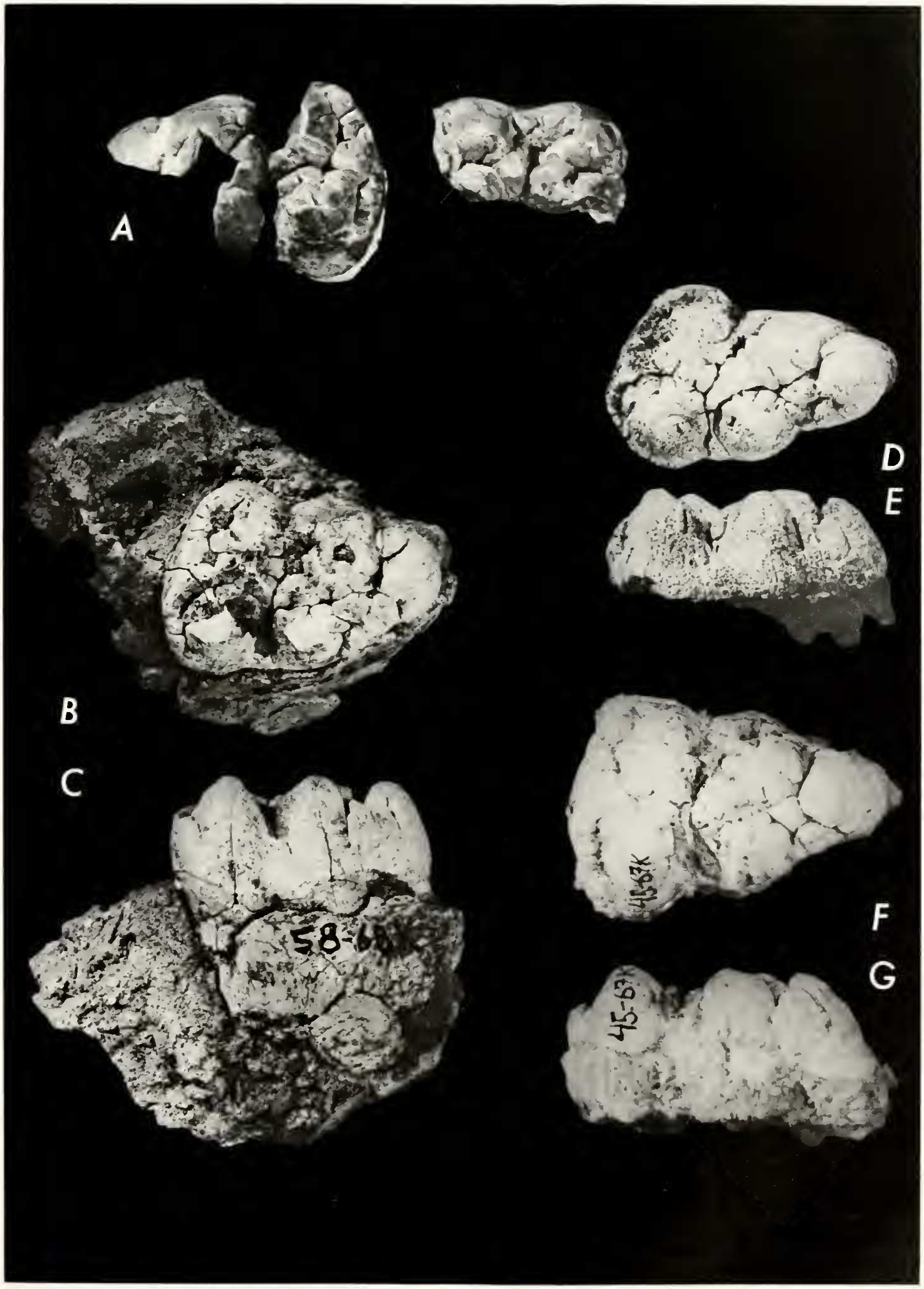

A
B
C
D
E
F
G
58-68
45-67K
45-67

Plate 26. *Notochaerus* cf. *capensis* Broom. **A**, **B**. Occlusal and right lateral views of damaged mandible, KNM-KP 226, from Kanapai. × ¼. **C**, **D**. Occlusal and right lateral views of incomplete mandible, KNM-KP 241. × ¼. **E**. Crown view of rather rolled piece of right mandible with RM_3 in moderately early wear, KNM-KP 210, from Kanapai. Nat. size. **F**. Crown view of well-worn LM_3 from piece of left mandible, KNM-KP 267A, from Kanapai. Nat. size.

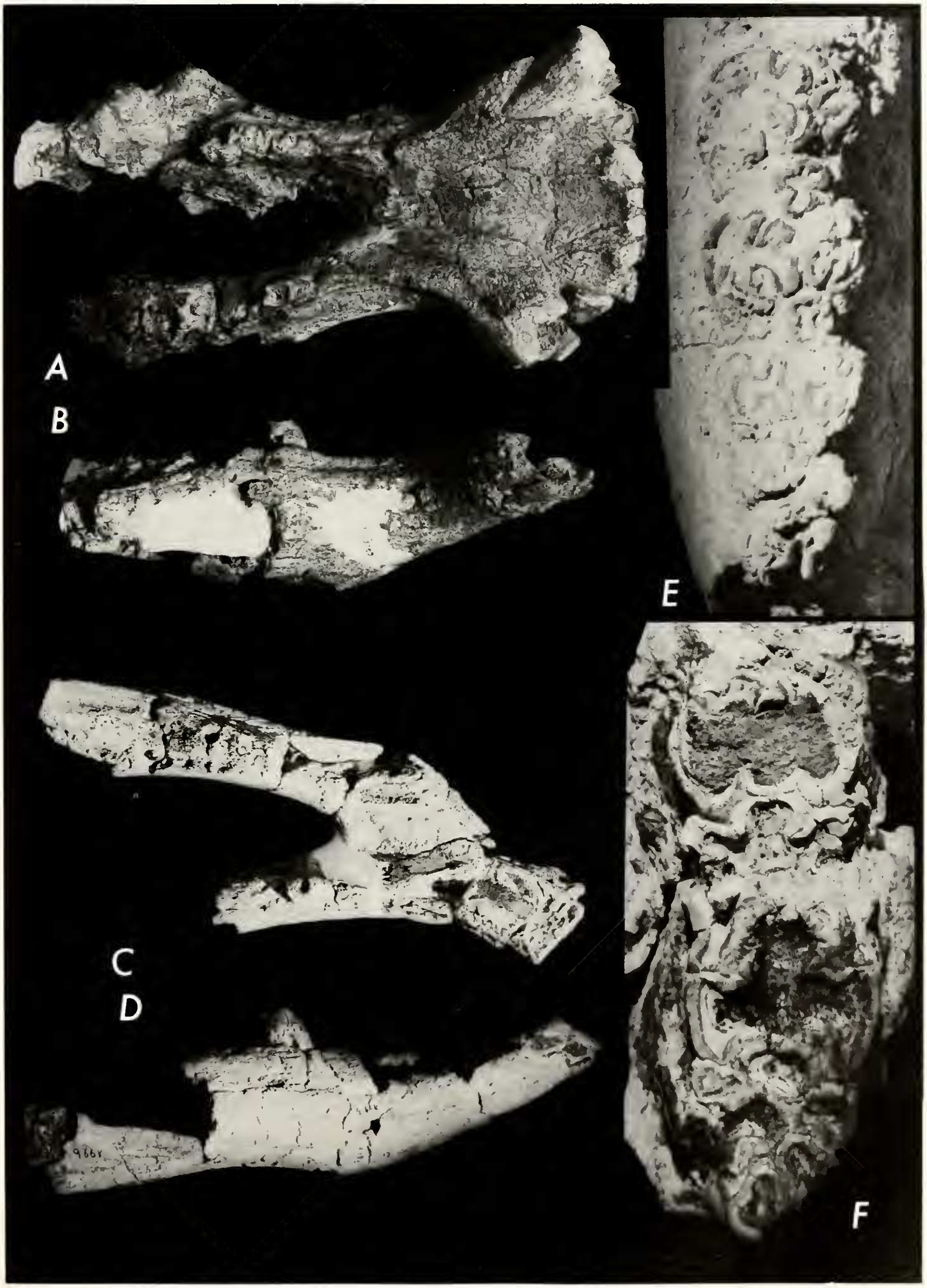

A
B
E
C
D
F

Plate 27. *Notochoerus* cf. *capensis* Broom. **A**. Inferior view of left upper canine, KNM-KP 267C, from Kanapoi. × ½. **B**. Dorsal view of two pieces of the snout of a disrupted skull, KNM-KP 242, associated with the mandible shown in Plate 26 C, D and with the zygomatic "knobs" in C and D below. The flange surrounding the base of the left canine is at the top and the premaxilla is at the right. × ¼. **C**, **D**. Lateral and (?) dorsal views of hollow bony zygomatic "knob" from the disrupted skull, KNM-KP 242. × ½. **E**. Palatal view of incomplete skull from the locality at Omo known as "White Sands," to show a zygomatic protuberance ("knob") similar to, but smaller than, the one from Kanapoi shown in C, D. × ¼.

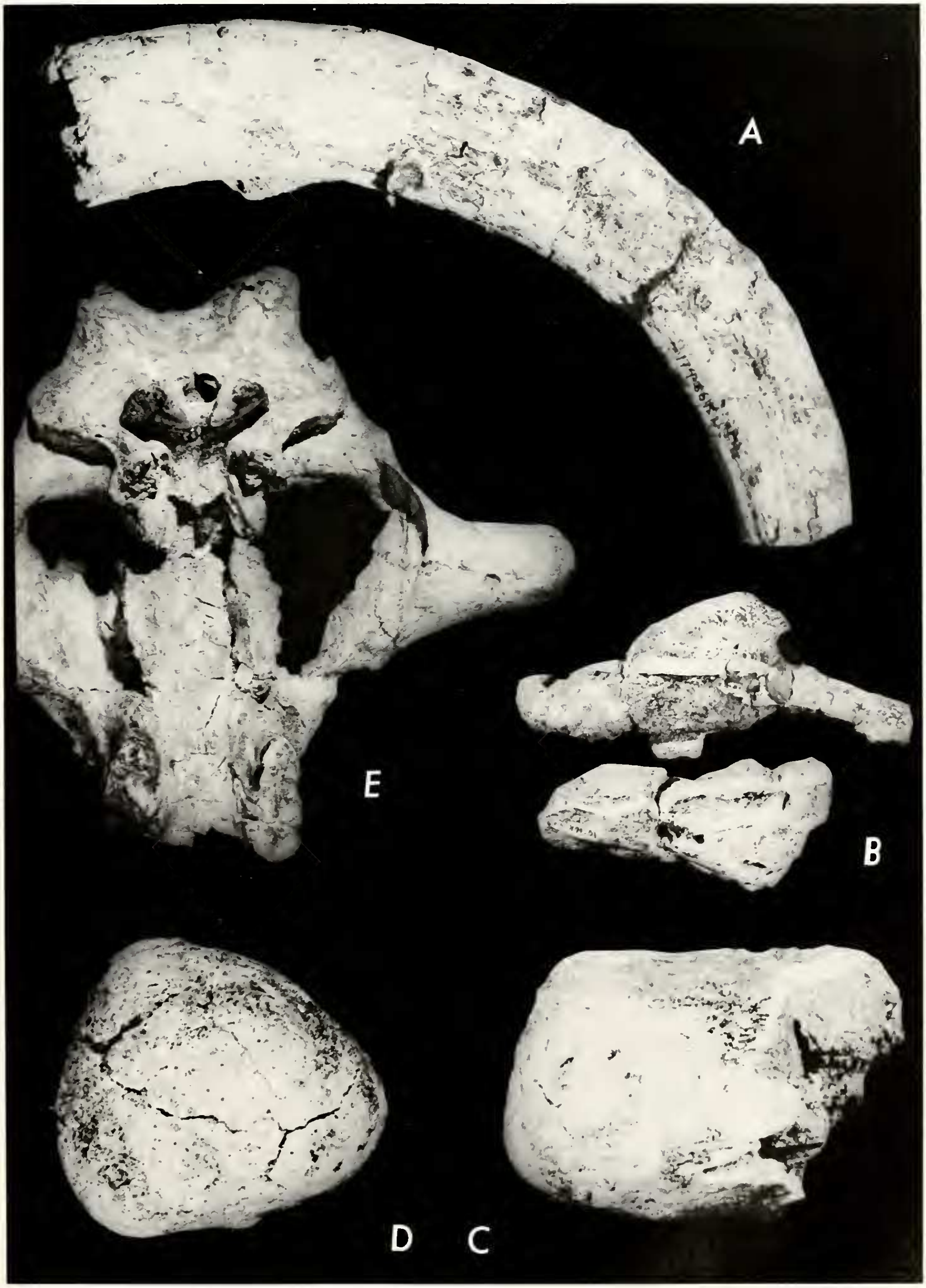

A
E
B
D
C

Plate 28. *Nyanzachoerus* sp. Occlusal view of mandible from Lothagam, KNM-LT 318, with much enlarged roots of P_3 and P_4 and remains of small LM_3. Nat. size.

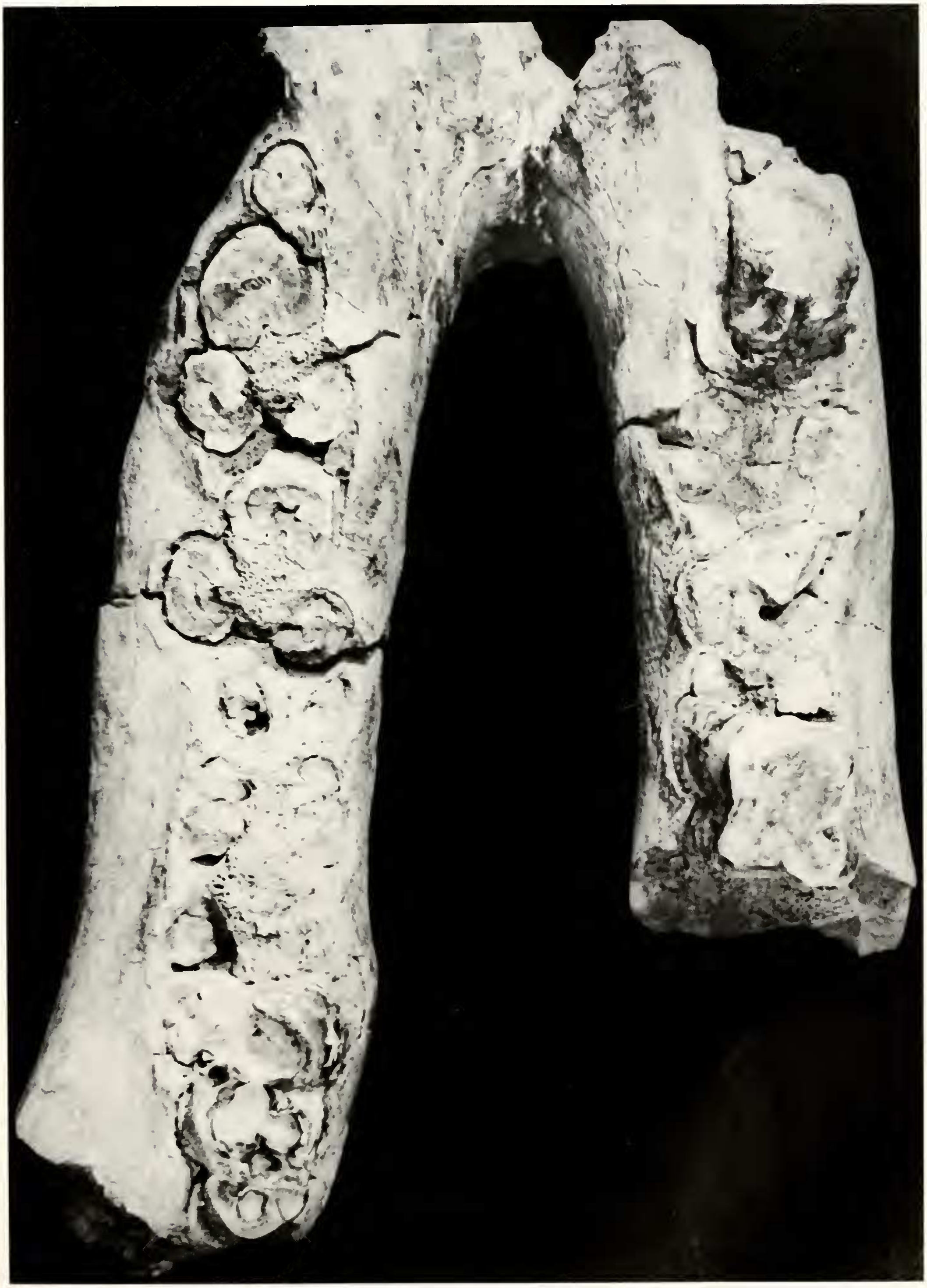
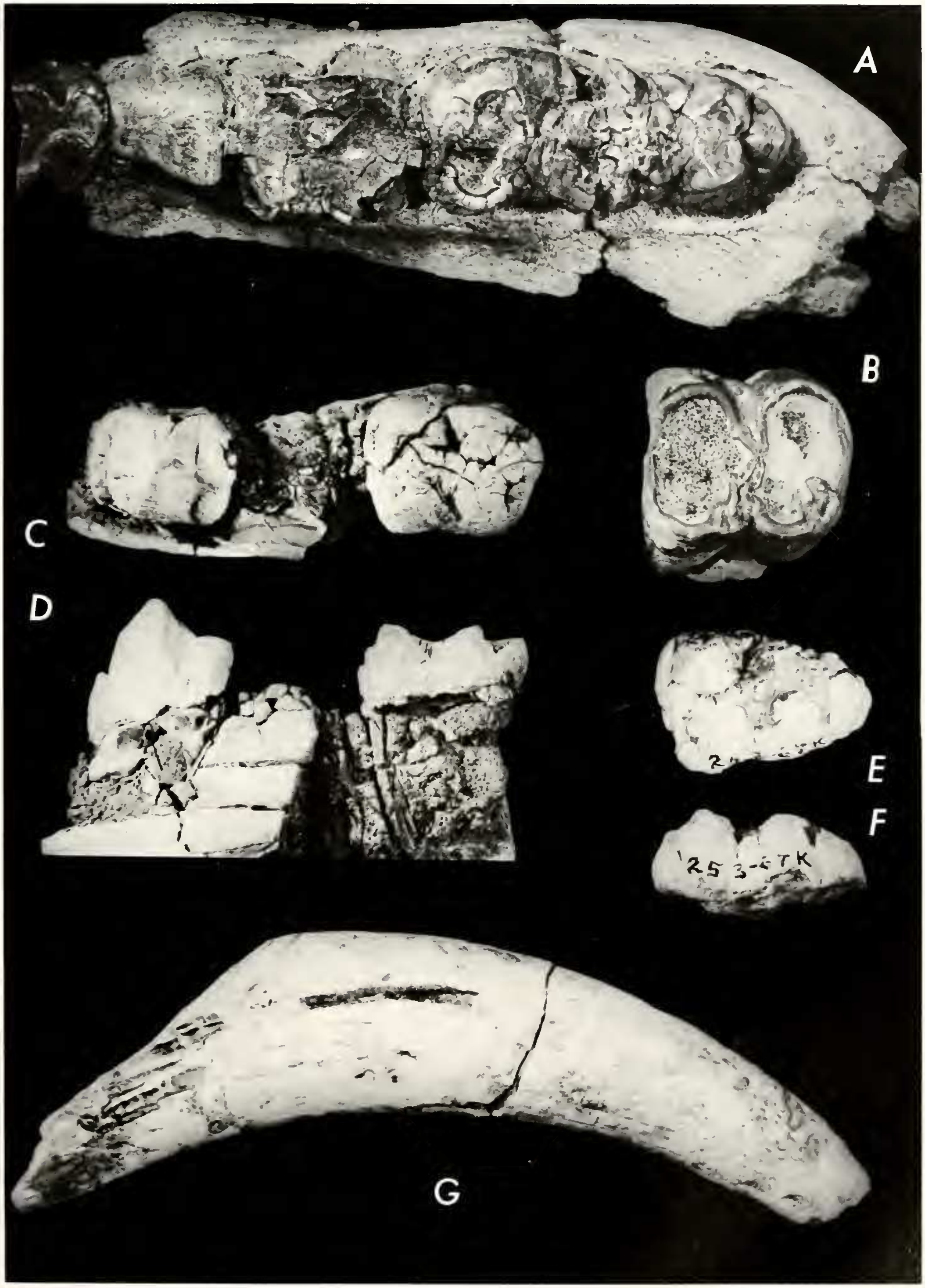


Plate 29. **A**. *Nyanzachaerus* cf. *pattersoni*. Occlusal view of piece of left mandibular ramus with LP$_4$ (damaged) to LM$_3$ (KNM-LT 285) from Member C of Unit 1 at Lothagam. **B**. *Nyanzachaerus* cf. *pattersoni*. Occlusal view of RM^2 associated with the mandible in A above (KNM-LT 285). **C**, **D**. *Nyanzachaerus* cf. *pattersoni*. Occlusal and outer lateral views of fragment of mandible with LP$_4$ and LM$_2$ (KNM-LT 294). **E**, **F**. Suid *indet*. Occlusal and inner lateral views of unworn LM^3 from Lothagam (KNM-LT 314). **G**. Suid *indet*. Dorsal view of right upper canine (KNM-LT 317) found at Lothagam with the holotype skull of *Nyanzachaerus tulotos*. All nat. size.


A
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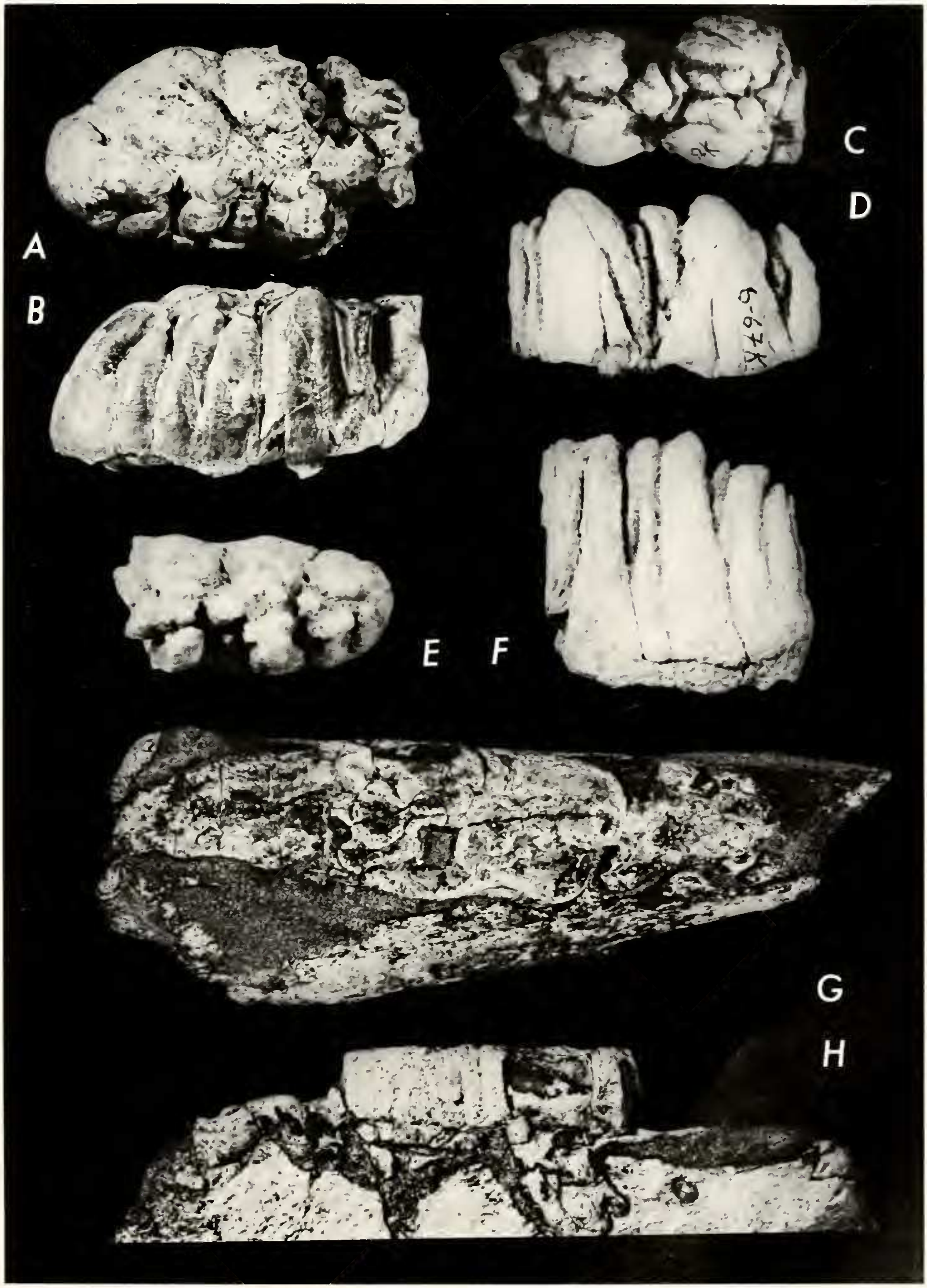
F
1253-67K
G

Plate 30. **A**, **B**. *Nyanzachoerus plicatus.* Crown and outer lateral views of upper LM^3 (KNM-LT 311) from near the top of Member C of Unit 1 at Lothagam. **C**, **D**. *Nyanzachoerus* cf. *plicatus.* Crown and inner lateral views of incomplete LM$_3$ from Ekora (KNM-EK 271). **E**, **F**. cf. *Notochoerus euilus.* Occlusal and inner lateral views of LM$_3$ (KNM-LT 297) from Unit 3 at Lothagam. **G**, **H**. *Notochoerus* cf. *euilus.* Occlusal and lateral views of piece of mandible with damaged well-worn RM$_2$ and incomplete RM$_3$ (KNM-LT 327) from the upper part of Unit 3 at Lothagam. All nat. size.


A
B
C
D
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H